CONSEIL PERMANENT INTERNATIONAL
POUR L'EXPLORATION DE LA MER
CHARLOTTENLUND SLOT — DANEMARK

JOURNAL DU CONSEIL

VOL. XXVI · NO. 3

PUBLIÉ PAR LE BUREAU DU CONSEIL

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EN COMMISSION CHEZ
ANDR. FRED. HØST & FILS
COPENHAGUE

SEPTEMBRE 1961

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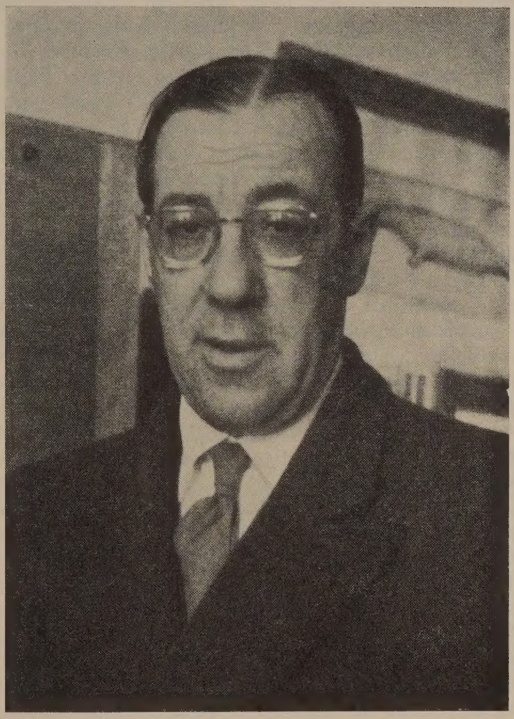
IMPRIMÉ AU DANEMARK
ANDELSBOGTRYKKERIET I ODENSE



Alfredo de M. Ramalho
1894—1959

Dr. Alfredo RAMALHO was born in Lamego on 26. April 1894 and died in Lisbon on 6. November 1959.

He came to Lisbon at an early age with his family and went to school at the Real Colégio Militar (his father was a Staff Officer in the army). Indeed he always showed in his bearing something of the traditional aplomb of a military man. However, on leaving school he did not follow his father's career. Not without some hesitation, he began to study medicine and in 1918 graduated at the Faculty of Medicine in Lisbon.

Since 1915 he had worked as an assistant in the Department of Histology and Embryology and in 1920 took a Doctorate in Medicine submitting as a thesis a "Contribução para o estudo do aparalho supra-renal", which was soon followed by a series of papers on this structure in fishes. Before the end of his University studies, and under the lead of his Professor of Histology at the faculty, he had laid the groundwork for the foundation of a marine biological station in Lisbon, in fulfilment of a recommendation by the Congress of Medicine in Lisbon in 1906.

In all this preliminary work, which led to the establishment of the Estação de Biologia Marítima at Dafundo in 1919, RAMALHO gave ample proofs of his energy, tenacity, and tact, as well as his scientific capabilities. Meanwhile, during a stay in France, he followed a course of studies in oceanography and marine biology at the Institut Océanographique in Paris and visited various centres where these sciences were practised. He took part in cruises on French research vessels and learned to carry out the oceanographic techniques at sea and in the laboratory. He also visited England and studied the methods used in sardine investigations, work on which he was to concentrate later on.

On his return to Portugal he was appointed, in 1914, as Director of the Estação de Biologia Marítima. His first task was to get hold of a ship and after considerable difficulties his efforts succeeded and "Albacora" was built in Norway. This ship was a sister-ship to the ketch "Armauer Hansen" of the Geofysisk Institutt, Bergen. During the months spent in Norway supervising the fitting of the scientific equipment in the ship, RAMALHO attended a series of lectures delivered by Professor HELLAND-HANSEN, whose friend he became. This proved to be most important to the course of RAMALHO's future scientific activities. His natural leaning to the mathematical treatment of great masses of numerical data – a somewhat unexpected and rather rare bent in a medical man – found expression in the methods on which physical oceanography rests.

After his return to Portugal, RAMALHO immediately started work at sea to train the naval crew of his ship. In spite of difficulties in obtaining assistants to help at sea, he started a systematic investigation of the physical and biological conditions along the coast of Portugal. This work was to lead to the "understanding of the biology of the ichthyological species (sardine, tunny, etc.) of interest to the fisheries of the country", according to the aim of the marine biological station at the time of its establishment.

The cruises carried out along the Algarve coast led, in 1927–28, to the exploration of the hydrographic conditions in the Straits of Gibraltar area, with a view to working out the water circulation there. This had been recommended in 1924 by the Comité du Plateau

Atlantique, at whose meetings RAMALHO had been present as an expert since 1922 and at which he now attended as a Delegate. The data he collected cleared the matter up, and the results were published in the ICES *Rapports et Procès-Verbaux*, vol. LXX, 1931. In the second World War his knowledge on this subject was put to advantage and in 1947 he was awarded the King's Medal in the Cause of Freedom. He had already been made a Chevalier de la Légion d'honneur by the French Government in 1934, and in 1949 he was further honoured by being made a Chevalier de l'Ordre du Mérite maritime.

The hydrographic explorations started in 1925 continued up to 1942. But the shortage of an adequately trained scientific staff was always a major problem which RAMALHO was never able to overcome. However, he never gave up. In 1952 the sardine work begun in 1947 was extended and an extensive programme of population work put under way. With a very limited staff he worked up all the biometric data collected up to 1956 and clearly intended to pursue these matters further before coming to any conclusions on so difficult a problem. However, his health was failing, and feeling unable to carry out the many duties he had, both at home and abroad, he decided to resign.

Before his resignation he had, however, in 1955, drafted the statutes of the Instituto de Biologia Marítima into which the Estação de Biologia Marítima had been re-organized in 1950. This was a heavy and laborious task and must have drained his capacities to their uttermost.

As a result of his resignation his association with ICES came to an end in 1956. He had joined the Council in 1922, first as an expert (1922–24), then as a Delegate (1926–56), he was a Vice-President of the Bureau (1948–51), and had acted as Vice-Chairman of the Atlantic Slope Committee, and (1955-57) as Chairman of the Scombriform Fish Committee. Here his good sense, scientific skill, and practical competence were highly appreciated, and his cordiality and gentleness praised by the many friends he had made and warmly kept in his affection.

For 32 years he used his great skill and energy in work for peaceful causes and in so doing showed the hard moral fibre and controlled enthusiasm of a pioneer. And a pioneer he was, in the lasting determination of his purpose. His country owes it to him that he was among those who took the first steps in the sciences of oceanography and marine biology, and thus opened up the way for the application of these sciences to Fisheries Biology.

Alberto Candeias

Toivo Henrik Järvi
1877—1960

The Finnish Delegate in the International Council for the Exploration of the Sea in the years 1920–1954, and internationally known fishery biologist, Professor Dr. Toivo Henrik JÄRVI, died at the venerable age of 83 years in Helsinki on 9. July 1960. He was born on 31. March 1877, matriculated in 1896, became Mag. phil. 1904, Philosophy Licensiate 1913, and was awarded Doctor degree 1914. His thesis was zoological, the two volumed "Das Vaginalsystem der Spanasiden".

Professor JÄRVI served as Senior Assistant of the Fisheries Inspector in 1908–18, Fish Counsellor 1918, Chief Director of the Board of Fisheries 1918–23, and from then on as Director of the Bureau for Fishery Investigations until 1947 when he retired on pension. He was also director of the zoological courses 1904–18 at the University of Helsinki, and Lecturer of Zoology in the Agro-Forestry Department of the University 1913–18. During 1944–59 he served as consulting member on the Oceanography Board of the Ministry of Commerce and Industry.

In his country Professor JÄRVI, as an experienced administrator, was given many responsible tasks in addition to his regular one. Amongst others, he was appointed member of the Finnish-Swedish Fishery Commission for the Tornio-Muonijoki river system 1920–24, and Chairman of the State Fishery Committee 1929–33, Chairman of the Fishery Society of Finland 1927–53, and Vice-President of Societas pro Fauna et Flora Fennica 1939–57. He was highly respected as a scientist, and was awarded honorary membership of this society in 1946. In 1919 he was invited to become a member of Finland's Academy of Science. Later, in 1946, he was awarded honorary membership in the "Vanamo" Society, and the following year honorary membership in the Finnish Society of Forestry Science, and also in the Fishery Society of Finland. Further he was awarded Medals of Honour from Finland and from Sweden.

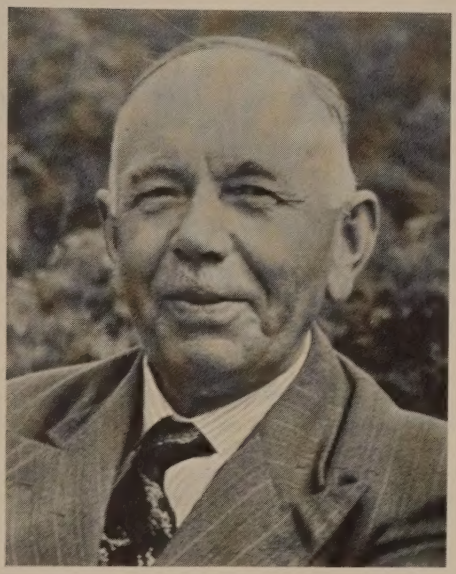
The scientific research work of Professor JÄRVI was broad and varied in scope. Of some of his more important work is his investigations on Cisco or Vendace (*Coregonus albula*) published in 1919 and 1924. In 1928 he published an extensive work entitled: "Über die Arten und Formen der Coregonen in Finnland". In 1932 he published in Finnish "Suomen merikalastus ja jokipyynti", describing the economically important fishes of Finland and the methods of fishing. A corresponding book in German was issued in 1934 entitled "Die Seefischerei von Finnland" in the series of "Handbuch der Seefischerei Nord-Europas". In conjunction with MENZIES he wrote in 1936, a valuable salmon research work "The interpretation of the zones on scales of salmon, sea trout and brown trout". Two years later Prof. JÄRVI published another notable salmon work entitled: "Fluctuations in the Baltic stock of salmon 1921–35". In 1940 appeared an investigation "Über den Maränenbestand in Pyhäjärvi". In later publications JÄRVI also discussed salmonids. Of these an investigation published in 1948 "On the periodicity of salmon reproduction in the northern Baltic area and its causes" is particularly worthy of mention. In 1950 he published "Die Klein-Maränen Bestände in ihren Beziehungen zu der Umwelt", and in 1958–59 an investigation entitled: "Über die Lachserträge im Oulujoki in den Jahren 1870–1948".

Professor JÄRVI devoted his leisure time to his hobby, heraldry, in which he was notably accomplished. He also collected an extensive

and valuable library in his home, which he shortly prior to his death bequeathed to the University of Turku (Finland). His extensive and varied studies and knowledge of mankind made him a pleasant and joyful companion who always had a fund of amusing tales of people and their undertakings. Fundamentally he was, nevertheless, first and foremost a hardworking and conscientious scientist, who day after day, year after year, laboured with his findings. For instance, he handled an enormous number of fish scales, more perhaps, than any other single biologist. In his salmon researches alone JÄRVI personally investigated the age and development of about 55,000 salmon. Many Baltic Sea salmon investigators have used this material to advantage in making comparisons.

Estimating Professor JÄRVI's life-work and accomplishments on the whole, one can say that he has been Finland's most outstanding fishery biologist to date.

Erkki Halme



Alf Nicolai Dannevig

1886—1960

Dr. philos. Alf Nicolai DANNEVIG died on 12. September 1960. He was born in 1886 in Hisøy, near Arendal. He entered the University of Oslo in 1904 where he studied zoology and took his degrees (Cand. real. in 1913, Dr. philos. in 1934). In 1911 he had succeeded his father Captain G. M. DANNEVIG as Director of the Sea-Fish Hatchery at Flødevigen, outside Arendal, a position he held until his retirement in 1957.

With his scientific training, DANNEVIG understood that experiments in the laboratory and investigations in nature were needed before an

answer could be given to the much disputed question if artificial hatching and rearing of fish larvae was of any use or not. Under his management therefore, the original sea-fish hatchery, founded by his father in 1882, has undergone a complete transformation and can now be described as a regular marine biological station, and the hatching and rearing of fish and lobster larvae is only a small part of the work carried on there. The station was taken over by the Department of Fisheries in 1918. A new building for well equipped laboratories was added in 1940 and a new sea-going research vessel was commissioned in 1950. As several ponds and an ample water supply are at hand, the station now has facilities for a very wide variety of research projects in marine biology and physical oceanography, both for staff members and for visiting scientists.

In his own studies, Alf DANNEVIG was active in a wide field for more than 40 years. His first studies were on the distribution of fish eggs and larvae in the waters along the Skagerak coast, in Canadian waters, and in the Lofoten area. In later years he conducted similar investigations in the Oslo Fjord. He made important contributions to our knowledge and understanding of the formation of summer zones and winter-rings in fish scales and otoliths, and he studied the influence of light and temperature on the number of vertebrae of cod and plaice. His studies of factors influencing the survival of fish and lobster larvae led to remarkable improvements in his techniques of hatching and rearing young fish and lobsters. Through field surveys he studied the age and growth of various fish stocks and he kept record of the numerical variations of fish larvae in nature as well as of the variation in temperature and salinity of coastal waters. Freshwater fish, such as trout and salmon, were also subjects for his interest and research.

During the years 1946 to 1953 Alf DANNEVIG attended regularly as an expert the meetings of the Transition Area Committee of the ICES. To fellow scientists in ICES a great number of his papers will, naturally, be well known. It remains to tell his many friends abroad that Dr. DANNEVIG also contributed considerably to the appreciation of marine biology in Norway by a great number of popular articles and pamphlets, which were widely spread and widely read.

All those who met Alf DANNEVIG in the Transition Area Committee, at the Flødevigen Station, or elsewhere, were impressed by his character, by his unfailing loyalty to the work begun by his father, and by his strong devotion to the marine sciences which he served so faithfully for half a century.

Johan T. Ruud

A Shallow Water Temperature Profile Recording System

By

George R. Rumney

Marine Research Laboratory, The University of Connecticut[1])

Introduction

At the University of Connecticut's Marine Research Laboratory, located on the shore of Mystic Estuary at the eastern end of Long Island Sound, apparatus has been installed for the semi-continuous recording of the sea water temperature profile. Temperatures are sounded at three levels in water ranging in depth from 2 m at mean low water to 2·7 m at mean high water. The values recorded are tabulated, graphically arrayed, and analysed in relation to recorded data on tidal rise and fall, atmospheric temperature, wind direction and velocity, precipitation, and sunshine duration. The virtually continuous record of sea water temperatures in profile is expected to fulfil a three-fold purpose: (1) to provide a long-range set of basic reference values, coupled with recorded atmospheric data, to which the results of short-range investigations can be related, in such fields as marine vertebrate and invertebrate ecology, bacteriology, algology, estuarine oceanography, biochemistry, and the like; (2) to provide raw material for the interpretation of long-range environmental variations important in ecological problems; and (3) to permit a determination of atmospheric influences on shallow water temperature fluctuations.

In the belief that others concerned with problems involving consideration of long-term shallow water temperature variations may be interested, a brief account of the apparatus and its performance is presented here.

Construction

Essentially the apparatus consists of a buoyant tubular spar, hinged at its concrete anchor, to which are attached three temperature probes transmitting a distance of 76 m to a recording potentiometer installed in the main laboratory building. The float is anchored about 32 m to seaward of the mean low water

[1]) Contribution No. 7 from the Marine Research Laboratory, The University of Connecticut, Noank, Connecticut.

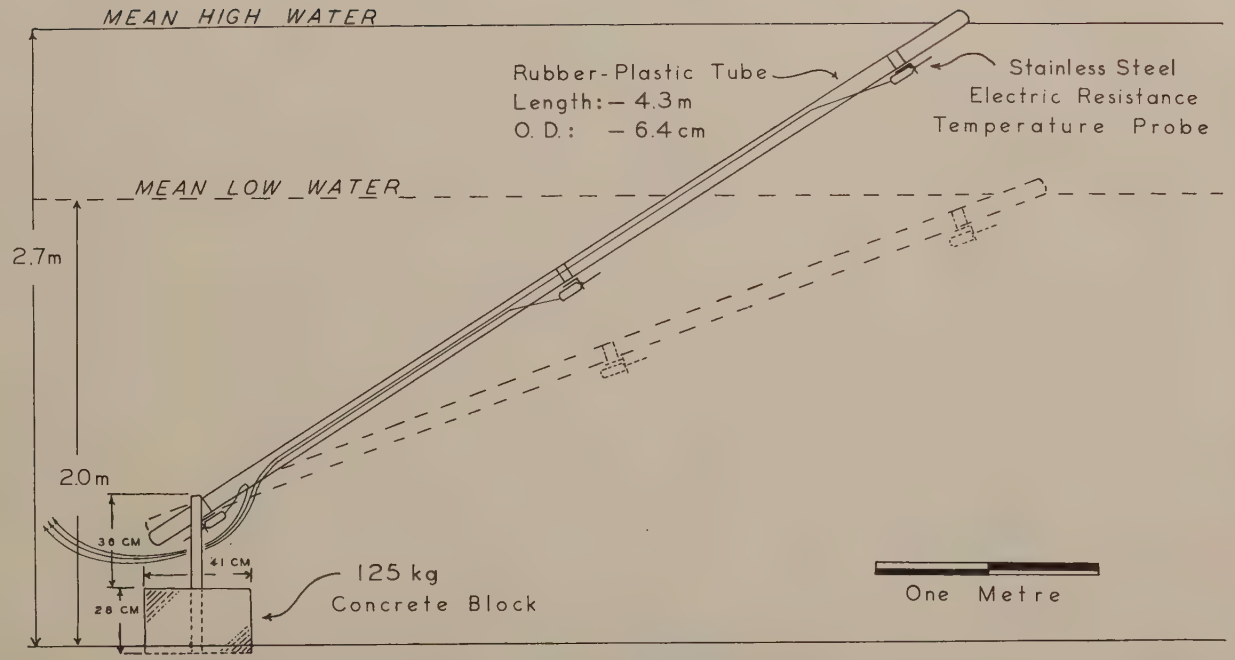


Figure 1. Shallow water temperature profile float.

mark, on the inshore side of a transverse section forming a T at the end of the laboratory dock. The spar float is a 4·3 m length of rubber-plastic pipe, 6·4 cm in outside diameter, sealed at both ends for buoyancy, and hinged at its lower end to brass and copper fittings embedded in a 125 kg concrete block (Figure 1). The pipe and plastic sealing compound have so far proved virtually non-reactive to local marine organisms and salt water.

Clamped to the float are three stainless steel electric resistance thermal probes, 6·4 mm in diameter and 10·2 cm long, the outer 4·1 cm of which is temperature sensitive. Each probe transmits by a three-wire, lead-sheathed, rubber-coated cable made fast along the outside of the float, and thence along the dock to the laboratory building. The stainless steel terminal housing in which each probe is connected with its transmitting cable is protected against the entry of salt water by three coats of nylon and an outer coating of the same corrosion-proof plastic compound used to seal the float.

This apparatus was installed in August 1958, and after more than two years of almost uninterrupted operation reveals no evidence of serious deterioration either in the float or its fittings. Properly coated probes have transmitted continously without failure from the very beginning. On two occasions, however, a probe had been improperly coated with protective material, allowing salt water to enter the cable terminal housing, which shorted the circuit. This difficulty has been easily avoided by applying the plastic compound with care. An annual haul-out has proved advisable for removal of organic fouling and inspection of the entire installation. Organisms are easily removed and have thus far not seriously damaged the apparatus.

Operation

Temperature values are recorded on a 30·5 cm strip chart, unrolling at a speed of 5 cm per hour, that requires changing once every thirty days. The chart is calibrated in unit degrees, and the temperatures transmitted are identified for each probe by number and discrete colour. The complete recording cycle for all three sensing elements is three minutes. Thus about 480 temperature soundings are recorded for each probe every twenty-four hours. Recorded temperatures are periodically checked by comparison with a set of laboratory thermometers having a known error and, within the limits of visual observation, no measurable drift has been detected in the thermal reaction of the system.

Rising and falling with the tide, the uppermost temperature bulb (No. 1) maintains an average position about 15 cm beneath the sea surface at all times, the lowest bulb (No. 3) about 40 cm above the bottom. The intermediate bulb (No. 2) varies in depth from about 115 cm beneath the surface at mean high water to about 75 cm at mean low water. The No. 1 bulb is prevented from emerging, even in the heaviest seas thus far experienced, by weighting the upper end of the float to provide a sufficiently sensitive rate of response to the vertical components of wave motion.

Characteristics of the water temperature experience at this point in the estuary – normal thermocline, isothermality, inversion, and heterothermal stratification – are clearly observable on the recorder chart with an accuracy of at least one-third degree Centigrade (Figure 2). The duration of a given temperature state, the rate and amplitude of temperature change at all levels,

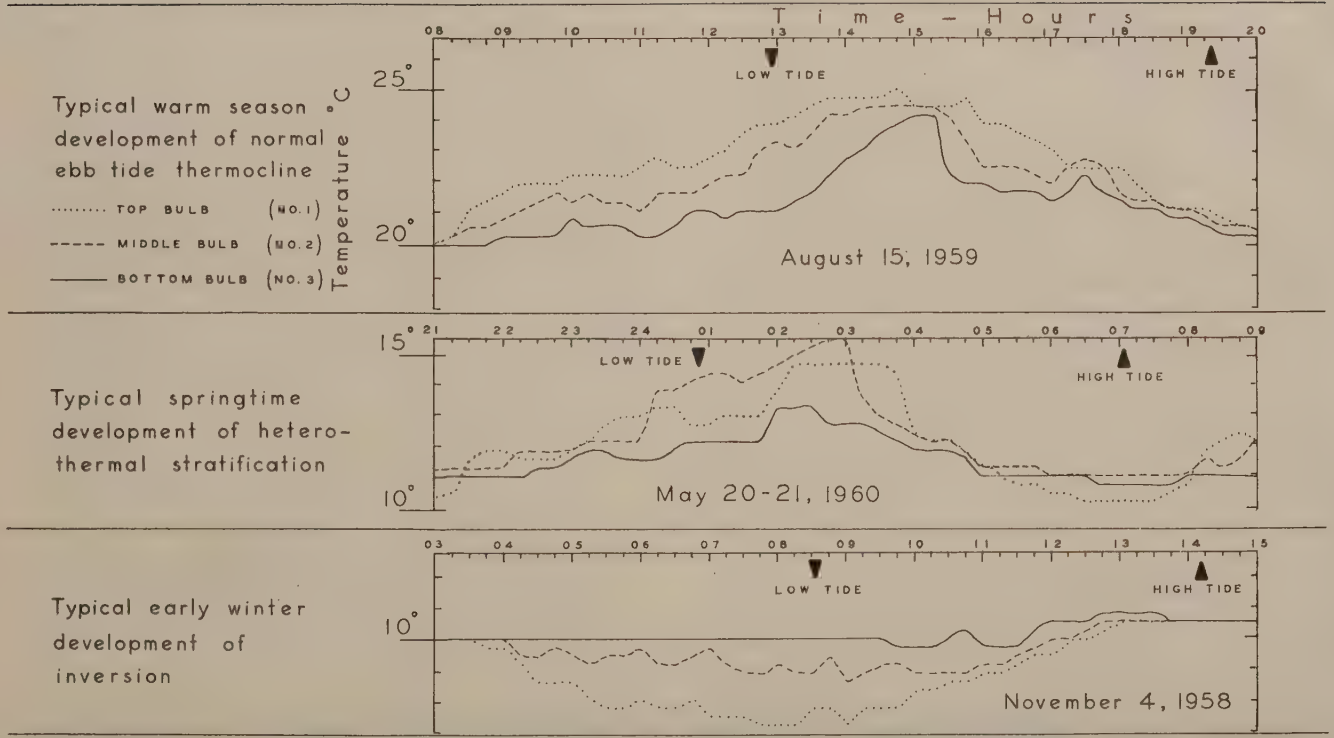


Figure 2. Characteristic fluctuations in the temperature profile at the point of observation.

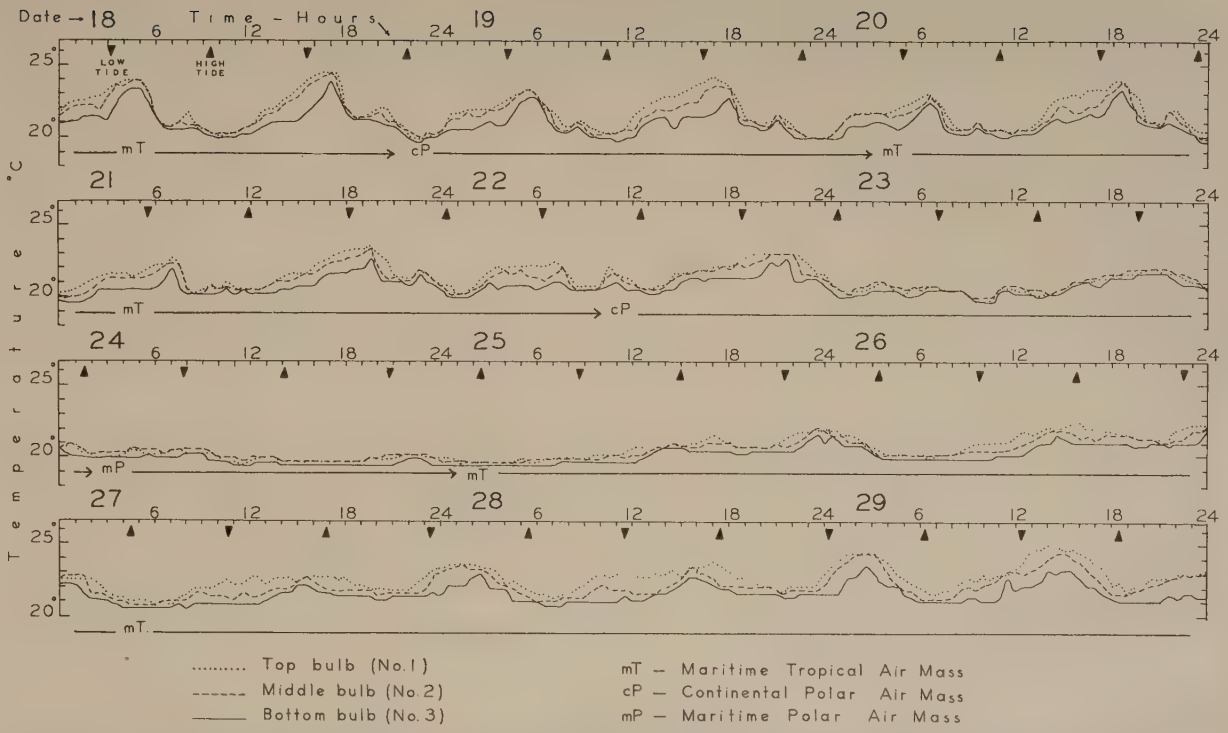


Figure 3. Periodic and non-periodic fluctuations in the water temperature profile at the point of observation, 18.–29. August 1959, shown in relation to the rhythmic occurrence of high and low tides, and the non-rhythmic passage of transient air masses. (See text for details).

as well as the slope of vertical temperature gradients and inversions, plus the changeful arrangement of heterothermal layers, are clearly portrayed. These are important advantages for analytical purposes since a given temperature state in the water column at the point of observation is rarely constant for more than a few hours, and temperature change is a primary environmental quality of the shallow tidal estuary.

Flood tide brings an onshore movement of water from greater depth that is thermally conservative, while ebb tide produces a seaward flow of thermally sensitive water from the shallows that is warmer in summer and colder in winter than water of deeper origin. Rhythmic temperature fluctuations set up by the twice-daily reversal of massive flow are thus fundamental tendencies of the water's thermal experience at the point of observation throughout the year. Superimposed upon these primary periodic variations is a less pronounced cycle, evident during the summer season, arising from the diurnal input and output of radiant energy from the sun, taking the form of a tendency toward slightly higher temperatures in the upper water layer (No. 1 bulb) on afternoon than on forenoon ebb tides. The frequency and amplitude of cyclical changes and the steepness of thermal gradients, and their time lag relationships with observed high and low tides, are readily apparent on the charted record, as illustrated for the period 18.–22. August 1959, in Figure 3.

Non-periodic fluctuations, also well revealed on the recorder chart, repeatedly interrupt the underlying temperature rhythms through the random occurrence of transient atmospheric situations. Further study of Figure 3, on which dominant air masses from 18.–29. August are plotted, shows the relationships between atmospheric change and sea water temperature behaviour. Warm, humid air of maritime tropical (mT) character dominated the weather of Mystic Estuary from 14. to 22. August 1959. Skies were either clear or only partly cloudy, allowing a high rate of insolation, winds were light, averaging about 8 km per hour, and were mainly from the south-west. Air temperatures remained almost constantly above those of the sea. A very weak cold front which crossed the area rapidly during the night of the 18th, although bringing a few hours of overcast skies and a trace of rain, scarcely depressed air temperatures and exerted only a negligible affect on the surface temperatures of the sea.

During the forenoon of 22. August, however, a very much stronger cold front ushered in a considerably colder, more persistent mass of dry, continental polar air (cP), changing in quality to the cool, moist air of maritime polar type (mP) after midnight of the 23rd. From around noon on the 22nd until after midnight on the 24th, skies were generally overcast, releasing occasional light rain, while winds were considerably stronger, averaging around 18 km per hour throughout the 23rd and 24th, and ranged in direction from north to south-east. Air temperatures remained constantly well below those of the sea. Sea water temperatures were almost isothermal, for all levels varied only slightly and averaged a good deal lower than during the preceding period of 14. to 22. August. Daily rhythms all but disappeared, and not until several days after the return of maritime tropical air, early on the 25th, were these and normal gradients gradually restored.

This highly generalized discussion of the recorded temperature profile is intended only to indicate the relative usefulness of the system. A meticulous analysis of the actual relationship between sea water and atmospheric parameters is expected to appear in a forthcoming article.

Acknowledgements

The author is indebted to Charles E. Rogers, formerly on the staff of the Marine Research Laboratory, for the design, construction, and installation of the anchored float described. Temperature bulbs and three-point recording potentiometer are produced by The Bristol Company, Waterbury, Connecticut.

Summary

Apparatus for obtaining a semi-continuous record of the temperature profile in shallow water at three levels at a single point of observation is described. The transmitting unit consists of a buoyant tubular spar on which are mounted three stainless steel electric resistance thermometer bulbs connected with a recording potentiometer. The virtually continuous record of values transmitted reveals the manner in which normal thermocline, isothermality, inversion, and heterothermal stratification develop in relation to the occurrence of high and low tides and changing atmospheric situations. The frequency, rate, and amplitude of both periodic and non-periodic fluctuations are clearly portrayed, along with the duration of successive temperature states, and other details of shallow water temperature experience.

Zooplankton in the Sargasso Sea off Bermuda and its Relation to Organic Production[1])

By

David W. Menzel

Bermuda Biological Station

and

John H. Ryther

Woods Hole Oceanographic Institution

Introduction

Zooplankton studies in the Sargasso Sea have been largely restricted to such collections and observations as were possible during oceanographic cruises crossing the area. While they have provided information concerning the abundance of animals at scattered times and places (e.g., LEAVITT, 1935, 1938; CLARKE, 1940; RILEY and GORGY, 1948), these investigations were not adequate for the purpose of describing seasonal cycles or even for establishing the fact that such cycles exist. More intensive studies by MOORE (1949) suggest that maximum populations occur in the spring, but even they do not encompass a sufficiently long period of time to provide a complete picture of seasonal trends.

Data collected during a period of 30 months from a total of 52 plankton tows, as part of an investigation of the plankton ecology of the Sargasso Sea off Bermuda, has now made it possible to define more clearly the seasonal cycle of zooplankton of this region. Correlary studies (MENZEL and RYTHER, 1960) permit a comparison to be made between primary organic production and the abundance and metabolic requirements of the zooplankton populations. While it is our intention, with the assistance of specialists, to enumerate and describe separately at least the quantitatively important components of the zooplankton, work upon that aspect of the problem has not yet progressed to the point where it warrants discussion here. This report, then, will be limited to a consideration of dynamic aspects of the zooplankton as treated collectively in terms of volume and weight.

[1]) Contribution No. 288 of the Bermuda Biological Station and Contribution No. 1121 of the Woods Hole Oceanographic Institution supported under Contract AT (30–1)–2078 with the Atomic Energy Commission.

Methods

Collections were made routinely, at intervals of approximately two weeks, at a station located 15 miles SE of Bermuda in 1500 fathoms of water. Standard oblique tows were made from a depth of 500 m, using a 0·75 m No. 2 plankton net with a meter wheel mounted in its mouth. Depth was estimated from wire angle. From time to time special tows were made with opening and closing nets at selected depth intervals to 2000 m, and on other occasions the standard No. 2 net was towed together with No. 8 or No. 20 nets for comparative purposes.

The samples were first split, half being saved for taxonomic studies. Displacement volume, dry weight, and ash-free dry weight of the second half were determined as indices of standing crop. Volumes were determined by the method of Yentsch and Hebard (1957). After volume measurements the samples were dried to constant weight at 60°C and then combusted in a muffle furnace at 800°C for determinations of dry weight and ash content respectively.

Comparative tows with nets of different mesh size

A series of simultaneous oblique (500–0 m) tows were made to compare the catching ability of No. 2 nets (0·366 mm aperture) with No. 8 (0·203 mm aperture) and No. 20 (0·076 mm aperture) nets. The results are given in Figure 1 in terms of displacement volume and ash-free dry weight of the paired tows. In general the plankton volumes taken by the different nets were remarkably similar, with no consistent differences between Nos. 2, 8, and/or 20 mesh. The ash-free dry weights (i.e., organic content) of tows made with Nos. 2 and 8 nets also did not differ significantly, but the weights of samples taken by the No. 20 net averaged 60% greater than that obtained by the No. 2 net.

The species composition of the plankton taken by nets of different mesh size has not yet been studied, but superficial examination of No. 2 net and No. 20 net tows revealed obvious differences in the respective populations. The finer net consistently caught more smaller organisms, particularly crustacea, as would be expected, but at the same time it captured far less of the larger animals (e.g., chaetognaths, siphonophores, medusae, fish larvae, etc.). The reason for this is not clear. It may be related to differences in the turbulence at the mouth of the two nets. However, essentially the same volumes were filtered by Nos. 2 and 20 nets, at least as far as was indicated by the net flow meters. The greater proportion of water in the larger gelatinous organisms, as compared to microcrustacea for example, undoubtedly explains the greater ash-free dry weight of the samples taken with the No. 20 nets.

Vertical Distribution

All plankton tows made during this investigation were taken during daylight hours, usually near mid-day. While the effects of diurnal migration were thereby held more or less constant, migratory animals could be expected to be located at or near their maximum depths when the samples were obtained. The main scattering layer in the Bermuda area lies at 400–600 m in daytime and the deep scattering layers may extend to 1000 m or more (Moore, 1950).

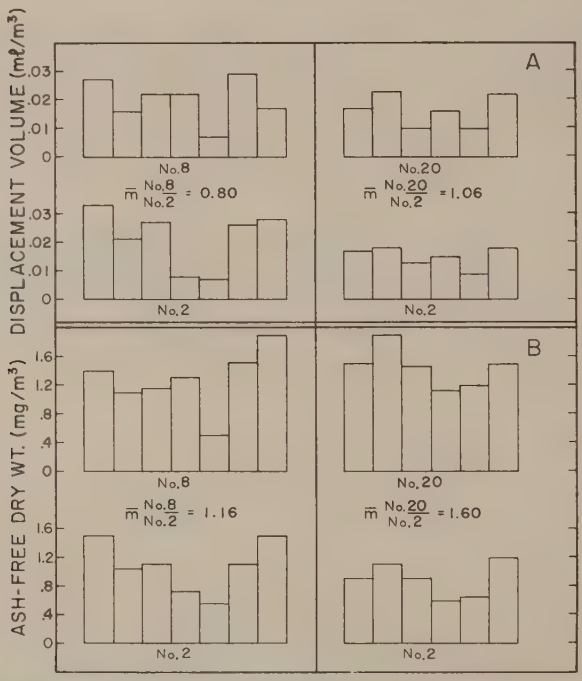


Figure 1. The comparison between (A) displacement volume and (B) ash-free dry weight of paired plankton tows with No. 2 versus No. 8 and No. 2 versus No. 20 mesh plankton nets.

Table 1

Vertical distribution of zooplankton

Depth interval (m)	Dry weight/depth interval (g)			Dry weight/m³ (mg)		
	June	Aug.	Feb.	June	Aug.	Feb.*
0– 100	0·49	0·19	0·17	4·92	1·90	1·16
100– 200	0·20	0·06	0·08	1·96	0·64	0·82
200– 300	0·12	0·06	0·15	1·22	0·61	1·46
300– 400	0·10	0·05	0·09	1·05	0·49	0·95
400– 500	0·09	0·15	0·09	0·93	1·54	0·93
500–1000*	0·77	0·35	0·90	1·55	0·69	1·21
1000–2000*	1·34	0·23	0·51	1·34	0·23	0·68
Total (g/m²)	3·11	1·09	1·99			
Mean (mg/m³)				1·85	0·87	1·03
% below 500 m	67·7	52·6	70·6			

* Depth intervals in February: 500 – 1250, 1250 – 2000 m.

To see whether our routine 500 m tows were missing a significant fraction of the zooplankton, and to investigate the vertical distribution of the organisms within discrete depth intervals, a series of tows were made with an opening and closing net, using essentially the same device as described by LEAVITT (1935), at depth intervals of 0–100, 100–200, 200–300, 300–400, 400–500, 500–1000, and 1000–2000 m. The results of three such series made in June and August 1959 and February 1960 (Table 1) reveal that an average of 63% of the zooplankton dry weight between 0 and 2000 m occurred below 500 m. The depth distribution of the zooplankton in terms of displacement volume and ash-free dry weight was almost idential to that found for dry weight, indicating that the major types of animals did not change greatly with depth.

The results of the three series were relatively consistent internally and in close agreement with LEAVITT (1938, Figure 4) who found an average of 59% of the plankton from 0–2000 m below 500 m in the Sargasso Sea north of Bermuda. Small to negligible fractions of the plankton were found by LEAVITT below 2000 m. Hence the values obtained by the standard 0–500 m tows may be increased by a factor of 2·75 to obtain an estimate of the total standing crop of zooplankton.

The Seasonal Cycle of Zooplankton Abundance

Zooplankton standing crops, in terms of displacement volume, dry weight, and ash-free dry weight beneath a square metre of surface as determined by the standard 0–500 m tows from November 1957 through April 1960 are reported in Table 2. The mean ratio for all the tows of displacement volume: dry weight: ash-free dry weight is 18:1·4:1.

For purposes of illustration, the seasonal cycle of zooplankton in terms of dry weight (0–500 m) is shown in Figure 2. It is clear that a spring maximum occurred during each of the three years. The magnitude and timing of these maxima paralleled to a close degree the spring flowering of phytoplankton, as will be discussed below. The spring maximum of 1958 (8·4 g/m^2) far exceeded those observed the following two years. Except for the spring period (March–June) the standing crop was low and almost constant, averaging less than 1·0 g/m^2, with no evidence of an autumn maximum.

Respiratory Requirement of the Zooplankton

Mixed zooplankton tows were diluted, dispensed in bottles and their oxygen consumption measured for periods of time ranging from 3 to 18 hours. A total of 55 measurements was made at eight times of the year (Table 3). Oxygen consumption was converted to carbon utilization assuming RQ = 1·0 and respiration is expressed as grammes carbon per gramme dry weight of zooplankton per day. There is considerable variability in the results, but no systematic variation with temperature was evident. The mean respiratory rate for 55 individual measurements was 0·125 g carbon/g zooplankton/day. The mean respiratory rate of a number of different marine zooplankton organisms, mainly copepods, reported in the literature is 0·103 g carbon/g zooplankton/day (Table 5), in good agreement with our results.

In view of the findings of CUSHING (1960) to the effect that the filtering rate

Table 2

Standing crop of zooplankton as determined from standard 0–500 m oblique tows with 0·75 m No. 2 net.

Date 1957	Displacement volume (ml/m³)	Dry weight (g/m³)	Ash-free dry weight (g/m³)	Date	Displacement volume (ml/m³)	Dry weight (g/m³)	Ash-free dry weight (g/m³)
Nov. 19	7·5	1·32	0·42	Apr. 7	24·0	1·36	1·13
Dec. 3	8·0	0·47	0·13	Apr. 17	12·0	0·88	0·78
1958							
Jan. 14	9·0	0·54	0·24	Apr. 30	9·5	0·61	0·50
Jan. 30	8·5	0·94	0·32	May 18	15·5	0·96	0·76
Feb. 11	18·0	2·51	0·45	May 28	12·5	0·92	0·73
Feb. 22	12·0	0·89	0·18	June 12	16·5	0·96	0·76
Mar. 25	86·0	5·97	3·57	June 26	10·5	0·66	0·53
Apr. 21	106·5	8·43	5·84	July 10	9·0	0·56	0·46
Apr. 29	21·5	1·83	1·42	July 22	12·5	0·91	0·76
May 19	7·0	1·05	0·39	Aug. 5	18·5	0·74	0·55
June 4	5·5	1·00	0·30	Aug. 25	9·0	0·71	0·56
June 18	12·5	1·44	0·94	Sept. 14	6·5	0·55	0·45
July 2	10·0	0·81	0·74	Oct. 6	5·5	0·44	0·88
Aug. 5	7·0	0·46	0·41	Oct. 27	4·0	0·37	0·34
Aug. 18	13·5	1·16	0·96	Nov. 8	5·5	0·46	0·37
Aug. 30	8·5	0·61	0·52	Nov. 24	4·5	0·35	0·28
Sept. 15	9·5	0·57	0·48	Dec. 10	13·0	0·83	0·60
Oct. 2	9·5	0·59	0·53	Dec. 21	8·0	0·61	0·46
Oct. 18	10·0	0·70	0·58	1960			
Nov. 1	5·0	0·43	0·36	Jan. 5	7·5	0·39	0·30
Nov. 14	14·0	0·88	0·79	Jan. 27	4·5	0·41	0·32
Dec. 2	6·0	0·37	0·34	Feb. 2	9·5	0·59	0·44
1959				Feb. 25	14·0	0·95	0·76
Jan. 2	9·0	0·66	0·58	Mar. 8	16·5	1·21	0·89
Jan. 30	7·0	0·55	0·50	Mar. 24	12·5	0·96	0·74
Feb. 26	11·5	0·65	0·57	Apr. 7	17·5	1·32	1·09
Mar. 25	23·5	1·95	1·75	Apr. 20	13·5	0·98	0·78
				Mean	14·0	1·08	0·75

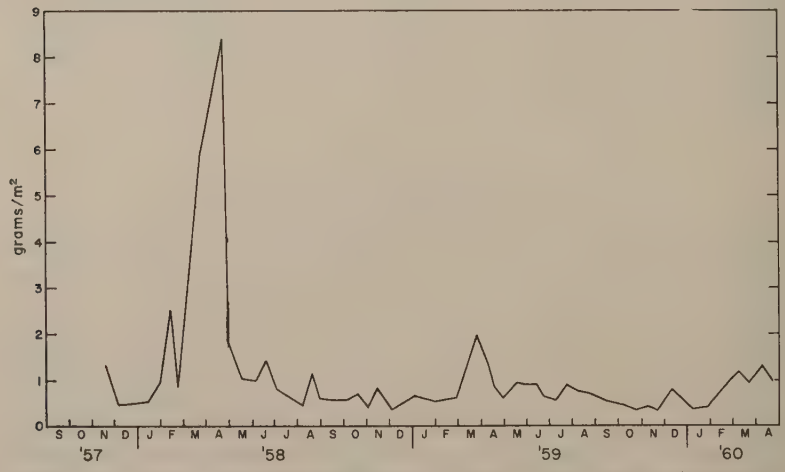


Figure 2. Dry weight of zooplankton from No. 2 mesh, 0·75 m, 0–500 m plankton tows, 1957–1960.

Table 3

Respiration of mixed zooplankton samples

Date	Temperature (°C)	Experiment length (hrs)	Number of measurements	Mean respiration (mgC/zooplankton/day)
1959				
Apr. 27.....	20·6	5	5	0·046
July 1	28·0	5	3	0·098
July 8	27·5	2	3	0·079
July 27	28·0	4	4	0·080
Aug.21.....	29·0	3·5	4	0·077
Oct. 28.....	25·0	5	4	0·123
Nov. 18	24·0	18	20	0·227
1960				
Apr. 19.....	20·0	3	12	0·087
			Mean	0·125

Table 4

Effect of the volume of container on the respiratory rate of mixed zooplankton, 18 hour experiment, 18. Nov. 1959, temperature 24·0°C

Volume container (ml)	Number of measurements	Mean respiration (mg C/mg zooplankton/day)
125	4	0·167
250	5	0·215
500	5	0·275
1000	3	0·239
2000	3	0·236

of marine zooplankton is proportional to the size of the experimental container, an experiment was carried out to determine whether respiration also is influenced by the volume of the experimental vessel (Table 4). For this experiment, individual copepods (*Paracalanus* sp. and *Labidocera* sp.) were selected out of a plankton tow and added to the vessels in numbers calculated to give the same density in every case. The density was lower than in the other experiments reported in Table 3, the experimental period considerably longer, and the resulting respiration rates appreciably higher. Below an experimental volume of 500 ml, there did appear to be reduction in the respiratory rates with the size of the vessel, but at 500 ml and above respiration remained relatively constant. The other measurements reported here were carried out in one litre containers.

It was intended that the experimental respiratory data be extrapolated to the environment in order to obtain an estimate of the metabolic requirement of natural zooplankton populations. In so doing, it seemed futile to attempt to correct respiration for temperature effects since the animals are distributed vertically within a temperature range which exceeds the seasonal range at the surface and migrate diurnally up and down within this range. The failure to observe any clear-cut temperature relation to respiration in our measurements, probably because of the crudity of the experiments, but possibly also due to temperature adaptation by the organisms, made it still easier to ignore this factor. We have therefore used a mean daily metabolic requirement in terms of carbon, of 12% of the dry weight of the zooplankton.

Table 5

Summary of reported respiratory rates of marine zooplankton
Carbon requirement calculated from oxygen consumption assuming RQ = 1·0

Organism	Reference	Respiration (g carbon/g zooplankton/day)
Calanus finmarchicus	MARSHALL *et al.* (1935)	0·026*
Centropages hamatus	ZEUTHEN (1947)	0·096*
Centropages hamatus	GAULD and RAYMONT (1953)	0·092*
Acartia clausi	CONOVER (1956)	0·116*
Acartia tonsa	CONOVER (1956)	0.154*
Marine copepods	ZEUTHEN (1947)	0·120*
Mixed zooplankton	RILEY and GORGY (1948)	0·120
	Mean	0·103

* Quoted from RICHMAN (1958) as recalculations of original data for 20°C assuming RQ = 1.

Net primary organic production and zooplankton metabolic requirements

Net primary organic production has been measured by the ^{14}C technique each time zooplankton tows were made, and has been discussed elsewhere (MENZEL and RYTHER, 1960, in press). The values are reproduced here (Figure 3), together with estimated values for zooplankton respiration (12% of the dry weight) based upon both measured standing crop (0–500 m) and estimated total standing crop (0–2000 m) obtained by multiplying the former by 2·75 as discussed above. It is assumed that the total respiratory requirement of the zooplankton populations falls within the range described by these two limits.

During most of the three-year period there was a striking agreement between net organic production and the metabolic requirement of the zooplankton. Clearly, the zooplankton is closely controlled by the availability of food during most of the year. The two high zooplankton values in March and April 1958, have been reported but are considered suspect since the volumes indicated by the net flow meter were exceptionally low. Without question there was a population maximum at that time but it is quite possible that gelatinous animals interfered with the turning of the meter, exaggerating the magnitude of the standing crop. Other than those values, the zooplankton appear to be closely controlled by the level of primary production, the spring flowerings of 1959 and 1960 being accompanied or closely followed by zooplankton maxima. The minor fluctuations in both zooplankton and primary production are probably no more than errors in measurement but may indicate short-term variations in both populations which are too rapid to be mutually influential. For example, there is the suggestion in the spring of 1960 that the short-lived high peak of primary production came and went too quickly to be reflected by the more slowly responding animal population.

In the relatively oligotrophic Sargasso Sea, then, there is little evidence of food surplus and wastage by the zooplankton, as has been proposed for more northern waters (e.g., HARVEY *et al.*, 1935; CUSHING, 1959). In the latter region, primary production is held in check by winter mixing and the resulting limitation of light. Nutrient levels within the euphotic zone far exceed anything observed in the Sargasso Sea. When stability of the surface layer permits phytoplankton growth, the spring bloom appears suddenly and the availability of algal food is

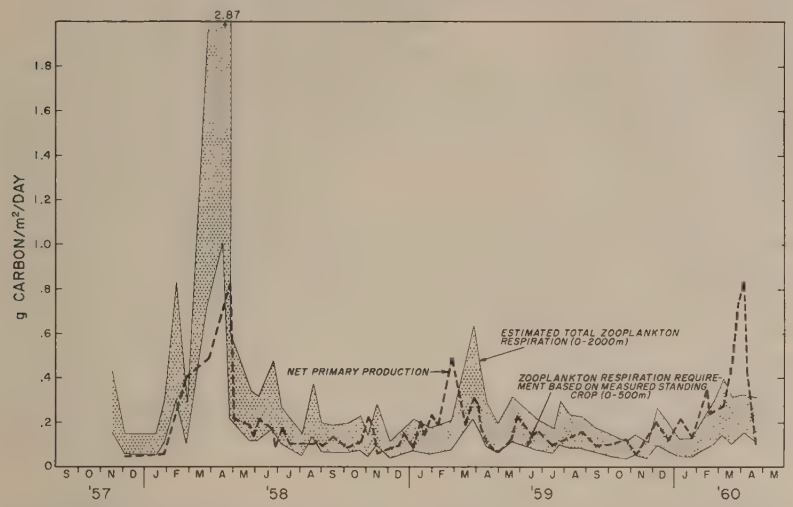


Figure 3. The relation between net primary production (broken line) and the metabolic requirement of the zooplankton represented as the stippled envelope. The lower limit being based on measured zooplankton populations 0–500 m and the upper limit based on the estimated total zooplankton population 0–2000 m.

greatly in excess of its demand by the lagging animal population. According to RILEY (1956) the zooplankton utilize no more than about 25% of the net primary production in Long Island Sound, the remainder sinking to the bottom or decomposing within the water in about equal proportions.

In the Sargasso Sea, by contrast, plant production proceeds throughout the winter unlimited by light but controlled in magnitude by the lower nutrient levels. The animals, by and large, keep up with the plants. Virtually 100% of the organic production is utilized by the relatively small and constant zooplankton populations. As CUSHING has pointed out, this is a highly efficient biological system and its efficiency is reflected in the small ranging populations of animals at the higher trophic levels. It is only in the inefficient eutrophic environments which irregularly produce large surpluses of basic food that large and dense populations of fishes can assemble and subsist.

Summary

1. Cycles in the abundance of zooplankton in the Sargasso Sea are characterized by maxima in the spring. Except for the spring period the standing crop is low and almost constant.

2. Experimental evidence indicates that the mean daily metabolic requirement in terms of carbon is 12% of the dry weight of the zooplankton.

3. There is striking agreement between net organic production and the metabolic requirement of the zooplankton. Clearly the zooplankton is closely controlled by the availability of food during most of the year. There is little evidence of food surplus and wastage.

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A Simple Screening Device for the Separation of Benthic Samples at Sea

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Introduction

In marine surveys of the macrobenthos where a large number of closely spaced stations are occupied, rapid and complete separation of animals from the sampled substratum is of importance if survey speed and sampling efficiency are to be obtained. Separation of the benthic animals contained in the sampled substratum can be accomplished in several ways, but perhaps the most effective method is sieving through a series of graded screens. The sizes and number of sieving screens and the type of substratum will, of course, affect the speed of sorting.

A device employing a pressurized water spray and mechanical agitation of the screens to accomplish sorting is described by HARTMAN (1955), and more recently, HOLME (1959) reports on a method of washing soil into suspension using a hopper equipped with water jets. Although this apparatus would make a thorough job of separation, the inherent complexity of these devices would in many instances limit their usage. A simpler non-mechanized device would be less subject to operational failures and would therefore be more practical for use at sea.

This paper describes in detail a simple and inexpensive sorting box which was found to be satisfactory during extensive field tests (Fig. 1).

Construction Details

Three trays were constructed by welding 5 cm × 5 cm × 0·6 cm angle iron to form rectangular frames (Fig. 2). The lower frame measured 61 × 91·6 cm

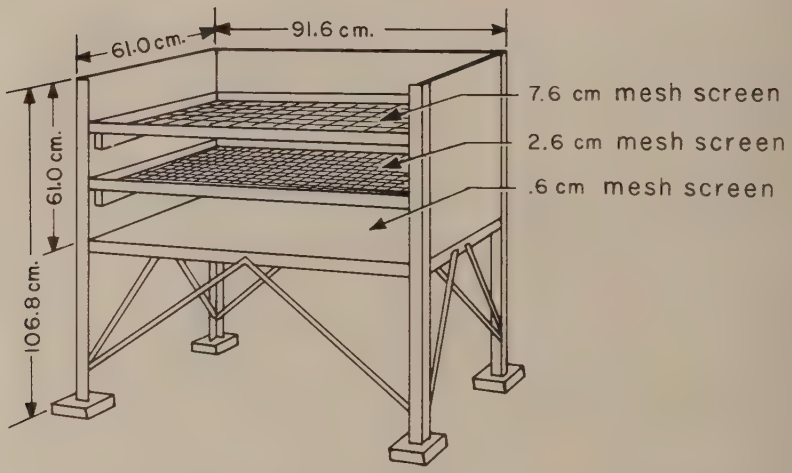

Figure 1. Perspective drawing of screening device with front panel removed.

Figure 2. Screening box before assembly.

Figure 3. Screening box in use aboard the Bureau of Commercial Fisheries exploratory fishing vessel "John N. Cobb".

while the middle and upper frames were 57·2 cm × 87·7 cm. Screen mesh of 7·6 cm, 2·6 cm, and 0·6 cm was inserted into the upper, middle, and lower frames respectively, and welded into position. Corner posts, 106·8 cm in length, were made of 5 cm × 5 cm × 0·6 cm angle iron. The bottom frame was bolted to the corner posts so that the lower sorting tray would be supported by 45·8 cm legs. Pieces of 2·5 cm × 0·5 cm angle iron 71·2 cm in length were then secured between the lower screen frame and the legs to make the sorting table rigid. Before assembly, all metal parts were galvanized to prevent corrosion. Permanent 1·9 cm plywood end sections, 57·2 cm × 71·2 cm were bolted to the upper sections of the corner posts enclosing the area from the lower screen to the top of the corner posts. Wooden screen supports which provided 25·4 cm vertical separation between the sorting frames were nailed to the plywood ends. When placed in proper position, the smaller size of the upper screen frames allowed the 1·9 cm plywood side sections to be dropped into place, completing the box (Fig. 3). Thus, both the upper two screens and both sides of the sorting box could be removed to provide ready access to the sorted animals.

Discussion

This screening box was first used in 1959 aboard the U.S. Bureau of Commercial Fisheries vessel "John N. Cobb" during a cooperative faunal survey conducted by the Bureau and the U.S. Atomic Energy Commission in the

south-eastern Chukchi Sea. Excellent results were obtained using the screening box to sort both otter trawl and dredge hauls. Catches with otter-trawl gear were handled in the box owing to the large predominance of benthic invertebrates. Dredge samples up to 0·5 m^3 containing mud could be washed in minutes, leaving only the animals they contained. These could then be easily removed from the trays, enumerated, and preserved for future study.

The efficiency of this device is complete with forms down to 5 mm in length. To effectively recover smaller animals a subsample can be sieved through a hand-box of mesh finer than 0·6 cm or processed using carbon tetrachloride or some other flotation technique. Larger animals such as tunicates, echinoderms, whelks, etc., are removed by the top screen along with any large rocks and debris included in the sample. The remaining material is separated according to size. Although a few of the softer-bodied animals may be damaged when separated in this manner, the amount of injury can be greatly reduced by careful application of the washing water under low pressure into the screening box. On boats not equipped with a controlled pressure system, a large diameter hose can be used with effectiveness.

A drawback of this method of recovery when used to separate grab samples is the loss of positional relationships of the animals with respect to their containing media. This is unavoidable, and only by careful observation at the time the sample is brought aboard can one expect to determine the natural stratification of organisms within the substratum.

A desirable refinement would be the addition of a sluice under the bottom screen of the box to return silt-laden washing water into the sea rather than onto the deck.

Summary

A screening box to separate benthic organisms from the sampled substratum was designed and used aboard the exploratory fishing and research vessel "John N. Cobb" during the summer of 1959. Construction details and a physical description are provided. A refinement to improve the efficiency of the described sorting device would be the addition of a sluice under the bottom screen of the box to return silt to the sea rather than onto the deck of the vessel. A major drawback to the sorting method for recovering benthic animals from grab samples is the loss of positional relationships of organisms with respect to their containing media.

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Der Detritus im Meere

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1. Einleitung

Schon seit langem kennen wir in der meereskundlichen Terminologie den Begriff des Detritus, mit dem der des Tripton synonym ist. Leider war über diesen Detritus außer seinem Namen bis vor 10 Jahren nicht viel bekannt. Mit Detritus bezeichnen wir alles das, was an zerriebenem Material im Meere schwebt. Wir verstehen darunter einmal die geformten Abbauprodukte der lebenden Substanz, dann aber auch Abbauprodukte toter Substanz, unabhängig davon, ob diese Abbauprodukte autochthoner oder allochthoner Natur sind. Für den Begriff des Detritus ist wichtig, daß es sich hier um Abbauprodukte handelt, die aus ihrem ursprünglichen Verband herausgerissen sind und wenn nicht gar von unregelmäßiger Form, so jedenfalls nicht mehr von jener Regelmäßigkeit wie sie im Verbande, beispielsweise der planktischen Diatomeen vorhanden sind. Man kann dem Begriff des Wortes Detritus einen verschieden weiten Umfang zuweisen: autochthoner Detritus im engsten Sinne ist all jene Substanz, die aus Lebendem in demselben Wasserkörper entstanden ist, das heißt ohne in vertikaler oder horizontaler Richtung verfrachtet worden zu sein. Im weiteren Sinne autochthon ist all jener Detritus, der in derselben Wassersäule vorkommt, das heißt also, der unter einer bestimmten Fläche entstanden ist, zum Beispiel unter einem Quadrat-Kilometer. Wir können den Begriff des autochthonen Detritus jedoch noch weiter spannen in dem Sinne, daß wir darunter alles zusammenfassen, was im Meere an Zerriebenem gebildet worden ist. Darunter fällt freilich nicht der vom Boden aufgewirbelte Detritus, der dem Wasser wieder beigemischt worden ist, denn dieser gehört eindeutig zur allochthonen Substanz, die nun freilich auch wieder ihre besondere Begrenzung hat. Eindeutig allochthon ist im Meere alles, was vom Lande her kommt, also entweder durch die Flüsse zugeführt wird oder über die Atmosphäre, wie zum Beispiel als Wüstenstaub oder Vulkanstaub, ins Meer gelangt. Allochthon ist auch alle jene anorganische Substanz, die beim Abtauen der Gletscher und der Eisberge ins Meer hineinkommt, wie zum Beispiel im Bereich des Ostgrönland- oder des Labradorstromes. Weiterhin sind die Aufbereitungsprodukte, die in der Erosionszone der Küste entstehen, zum Beispiel in umfangreichem

Maße an unseren Steilküsten bei Hochwasser oder ständig, wenn auch in geringerem Maße, an den atlantischen Steilküsten, um nur zwei Beispiele anzuführen, allochthoner Natur. Wir haben freilich im Meere auch einen autochthonen anorganischen Detritus, der einmal biotischen Ursprungs ist, wie zum Beispiel die Kalkschalen der Coccolithophoriden oder die Silikatschalen der Diatomeen.

Es ergibt sich ferner die Frage, welche materiellen Eigenschaften der Detritus eigentlich besitzt. Wir können zunächst eine rein mechanische Beschreibung vornehmen: wir erblicken in ihm unregelmäßig geformte, kleine Partikel mit zum Teil sehr stark vergrößerter spezifischer Oberfläche, Partikel, an denen man oft nur mit Mühe bei hoher mikroskopischer Vergrößerung ihren Ursprung erkennen kann. Zum Begriff des Detritus gehört noch, daß dieser im Wasser schwebt oder sich zumindest längere Zeit im Wasser flottierend erhalten kann, daß wir also nicht schon in jedem zerrissenen Fisch Detritus erblicken.

Die chemische Natur des Detritus muß entsprechend seiner Herkunft außerordentlich unterschiedlich sein. Wir kennen zunächst einmal den jungen Detritus, wie er beispielweise aus frisch ausgeschiedenen Verdauungsprodukten stammt, die nicht vollständig abgebaut sind. Dann unterscheiden wir als anderen Extremfall den schwer abbaubaren Detritus, der sowohl pflanzlicher als auch tierischer Herkunft sein kann und beispielweise aus Zellulose, aus Pektin und aus Chitin bestehen kann. Man kann sich aber sehr wohl vorstellen, daß zum Beispiel auch tote Phytoplankter im stark beschädigten Zustand, in dem sie außer ihren Schalen noch Reste von Plasmasubstanz tragen, schon mit zum Detritus gehören und eine außerordentlich heterogene chemische Zusammensetzung zeigen. Mit dieser Definition ist auch schon über die Herkunft des Detritus etwas gesagt, der entstanden ist als Produkt autolytischer Zersetzungsvorgänge pflanzlicher und tierischer Wesen sowie aus Resten von Verdauungsvorgängen, wie zum Beispiel aus aufgelösten Kotballen von Copepoden.

Es erhebt sich jetzt weiterhin die Frage, wie groß dieser Detritus ist. Wir verfügen dabei über sehr wenige Angaben, sofern wir uns an die allgemeine Definition halten. Es ist aus der Arbeit von GILLBRICHT (1951) bekannt, daß dieser Detritus in der westlichen Ostsee in seinen Beobachtungszeiträumen eine mittlere Größe von 20 µ besaß. WYRTKI (1950) beobachtete unabhängig von GILLBRICHT die Größe des Detritus zu 15 µ Durchmesser.

Auf die Rolle des Detritus im Meere hat zuerst LOHMANN (1908) hingewiesen in seiner berühmten Untersuchung "Zur Feststellung des vollständigen Gehaltes des Meeres an Plankton". Er bediente sich dabei zum ersten Mal in umfangreichem Maße der Planktonzentrifuge, mit der er auf einer Station vor der Kieler Förde jeweils 100 l aus verschiedenen Tiefen bearbeitete. LOHMANN hat in einer Tabelle (Tabelle 1) für die Monate August 1905/August 1906 die Masse der Pflanzen und Tiere bestimmt. Dabei ergibt sich im August ein Maximum an Pflanzen von 109 mm^3/100 l und im Februar ein Minimum mit 3·5 mm^3. Das Maximum an planktischen Tieren hat LOHMANN im September gefunden mit 68 mm^3 und das Minimum an Zooplankton mit 13 mm^3 im April. Diese gegenseitige Verschiebung der Maxima und Minima weist schon auf den Nahrungszusammenhang hin. LOHMANN hat diese Gesamtzahlen noch einer weiteren Untersuchung unterzogen. Er hat alle Phytoplankter, die offensichtlich durch ihre Größe und ihre Sperrigkeit nicht als Nahrung für

Tabelle 1

Jahresgang des Plasma Volumens von Phyto- und Zooplankton (LOHMANN, 1908 Station Laboe, 1905–1906), in $mm^3/100$ l

	Monat					
	August	September	Oktober	November	Dezember	Januar
Masse der Pflanzen	**109**	82	43	26	10	5·4
Tiere	46	**68**	45	37	25	16
Als Nahrung verfügbare Produzenten	**35**	27	14	9	3·5	3
Tagesbedarf der Konsumenten	6	8	5·5	4·5	2·5	**1·8**
Differenz	+29	+19	+8·5	+4·5	+1·0	+1·2

	Februar	März	April	Mai	Juni	Juli	August
Masse der Pflanzen	**3·5**	10	39	46	62	52	51
Tiere	15	19	**13**	49	22	32	32
Als Nahrung verfügbare Produzenten	1	3	13	14	20	17	16
Tagesbedarf der Konsumenten	**1·8**	2·4	2	5·5	4·0	4·5	4·3
Differenz	÷0·8	+0·6	+11	+8·5	+16	+12·5	+11·7

Zooplankter geeignet sind, aus den Berechnungen ausgeschieden und fand dann folgende Zahlen: für August ein Maximum mit 35 mm^3 und ein Minimum im Februar von 1 mm^3 an Phytoplanktern, die unmittelbar als Nahrung zur Verfügung stehen. Weiterhin hat LOHMANN den Tagesbedarf der Zooplankter berechnet. Er kommt dabei auf 8 mm^3 Nahrungsbedarf pro Tag und 100 l Volumen im September and auf 1·8 mm^3 im Januar und Februar. Bei einer Gegenüberstellung der verfügbaren Nahrung und des Nahrungsbedarfs ergibt sich als Differenz meistens ein Überschuß an verwertbaren Phytoplanktern mit Ausnahme von Februar, wo ein erhebliches Defizit auftritt, und zwar von 1·2 und 0·8 $mm^3/100$ l. Da aber in diesem Monat noch verhältnismäßig viel Zooplankton existiert (Tabelle 1, Zeile 2), müssen die Zooplankter diese Zwischenzeit mit dem Nahrungsdefizit offensichtlich gut überstanden haben. Das erklärt LOHMANN nur durch die Existenz des Detritus, der während dieser Zeit als Nahrung zur Verfügung stand. Als Jahresdurchschnitt für die verwertbaren Produzenten errechnet LOHMANN 13·5 mm^3 und als Tagesbedarf für den Jahresdurchschnitt der Konsumenten 4·1 $mm^3/100$ l. Daraus ergibt sich ein Überschuß von 9·4 mm^3/Tag, also eine sehr erhebliche Menge, die nicht vom Zooplankton aufgenommen wird und daher anderweitig zur Verfügung steht, insbesondere den Benthosorganismen. Ein großer Teil davon wird unmittelbar sedimentieren, wofür wir in den obersten Bodenschichten den besten Beweis haben. Zur Methodik von LOHMANN muß noch erwähnt werden, daß er den Tagesbedarf aller Metazoen zu $\frac{1}{10}$ ihres Volumens ansetzte, während er annahm, daß alle Protozoen sogar die Hälfte ihres Volumens als Tagesration an Phytoplankton gebrauchen. Als Vermehrungsrate für dieses Phytoplankton setzt er für die Wintermonate den Faktor 1:3, das heißt, daß ein Bestand sich in drei Tagen verdoppeln würde, eine Annahme, die nach unseren heutigen Kenntnissen etwas zu hoch liegt, jedenfalls nicht in allen Jahren regelmäßig erfüllt sein dürfte.

Auf die große Rolle des Detritus weisen auch die Untersuchungen von

MARSHALL und ORR (1923) hin. Sie finden, daß im Januar über 40% aller Individuen von *Calanus finmarchicus* nur Bruchstücke von Phytoplanktern im Darm aufwiesen, während um diese Zeit weniger als 20% eine erkennbare Nahrung wie Diatomeen, Dinoflagellaten usw. zeigten.

Zu Zeiten der stärksten Planktonentwicklung, also im Frühjahr und im Herbst, hat ein Minimum der Tiere keine geformte Nahrung im Darm, während im Juli und August ein etwas höherer Prozentsatz der Tiere entsprechend dem geringeren Angebot an Phytoplankton geformte Nahrung im Darm enthält. Durch diese beiden Beispiele kann indirekt auf die große Bedeutung des Detritus für die filtrierenden Organismen im Pelagial des Meeres geschlossen werden.

ZOBELL (1950) hat in seinem Buch mehrfach auf die Rolle des Detritus für die Entwicklung der Bakterien hingewiesen. Die Bakterien im Meere können normalerweise bei den darin herrschenden Konzentrationswerten für gelöste organische Substanz nicht ohne weiteres im freien Wasser existieren. Vorwiegend durch den Detritus ist es ihnen möglich, sich zu sehr starker Volkszahl zu entwickeln, denn der Detritus wirkt im freien Wasserraum als Adsorbens für gelöste organische Substanz. Das wirkt sich dahin aus, daß die Oberfläche der Detrituspartikel mit einem verhältnismäßig starken Konzentrat der organischen Substanz behaftet ist. Dieses Oberflächenhäutchen jedoch bildet für die Bakterien die geeignete Nahrung, so daß sie sich in größerer Zahl entwickeln können. JANNASCH (1954, 1959) hat in zwei Arbeiten, in denen er sich mit dem Bakterienbesatz des Detritus im Golf von Neapel befaßt, sehr schön zeigen können, wie stark der Detritus von Bakterien besetzt ist. Als weiteres Adsorbens für die gelöste organische Substanz dürfte auch die stellenweise in großer Menge im Meere vorkommende Feintrübe in Betracht kommen, eine Substanz, die zum Beispiel ARMSTRONG und ATKINS (1950) im Englischen Kanal besonders untersucht haben. Leider wissen wir bisher nur noch zu wenig über die wirklichen Vorgänge an der Oberfläche des Detritus, zum Beispiel in welcher Menge dieser, vielleicht sogar selektiv, organische Substanz zu adsorbieren vermag.

2. Methoden zur Bestimmung des Detritus

Die Methoden zur exakten Bestimmung des Detritus sind außerordentlich schwierig. Wir können selbstverständlich zunächst einmal rein mikroskopisch am sedimentierten Material die Teilchengröße, -form und -anzahl bestimmen. Es eignet sich hierfür besonders gut die Utermöhl-Methode, die es — mit gewisser Vorsicht angewandt — ermöglicht, allen Detritus, der schwerer als Wasser ist, sofort nach dem Sedimentieren in denselben Gefäßen mikroskopisch zu untersuchen. Selbstverständlich kann man auch mit einer Zentrifuge das Gleiche erreichen, wenn auch auf etwas umständlichere, zwar schnellere Art und Weise. Die Utermöhl-Methode bietet uns heute einen weiteren großen Vorteil; man kann mit sehr geringem Zeitaufwand von den sedimentierten Proben Mikrophotographien herstellen, die man hinterher vergrößern und an denen man — natürlich unter der Voraussetzung eingehender Kenntnis der Formen des lebenden Planktons — die Detrituspartikel erkennen kann. Diese Detrituspartikel sind nachher zählbar mit Hilfe eines in jüngster Zeit von Carl ZEISS gebauten "Teilchengrößen-Analysators", bei dem durch eine halbautomatische Methode der Durchmesser der einzelnen Partikel zusammen

mit ihrer Zahl festgehalten wird. Diese Methode über das Mikroskop, die Mikrophotographie und den Teilchengrößen-Analysator gibt uns heute ein vielversprechendes Mittel in die Hand, eine unmittelbare, quantitative Erforschung des Detritus durchzuführen.

Außer dieser mikroskopischen Methode gibt es noch eine gravimetrische, die man mit der mikroskopischen kombinieren kann. Man bestimmt das Sestongewicht und zieht von diesem die mikroskopisch ausgezählten und nach ihrem Volumen errechneten lebenden Partikel ab. Man kann dabei selbstverständlich nur mit Mittelwerten arbeiten, die im Einzelfall gewiß einer mehr oder minder erheblichen Korrektur bedürfen, uns aber zumindest die Größenordnung angeben, in der sich die einzelnen Komponenten halten. Weiterhin verfügen wir noch über eine gravimetrisch-chemische Methode zur Ermittlung des Detritus. Man bestimmt die Menge des Sestons nach bekanntem Verfahren (KREY, 1950) und zieht von diesem Seston die auf chemischem Wege ermittelten Werte für das Gewicht des Phytoplanktons und das Gewicht des Zooplanktons ab. Dabei läßt sich die Menge des Phytoplanktons mit Hilfe von Mittelwerten seines Chlorophyllgehalts (HAGMEIER, 1961; KREY, 1958) oder in jüngster Zeit auch auf Grund der physiologischen Bestimmung des Phytoplanktons mit der ^{14}C Methode ermitteln. Die Menge des Zooplanktons wird mit der Eiweißmethodik (KREY, BANSE und HAGMEIER, 1957) bestimmt: man analysiert den Gesamtwert des Eiweißgehaltes des Sestons, zieht davon das Phytoplanktongewicht ab und erhält so durch Differenzbildung einen zumindest größenordnungsmäßig richtigen Wert für das Zooplankton. In diesem Zooplankton ist freilich der Wert für die auf dem Detritus wachsenden Bakterien mit enthalten. Gleichfalls sind darin enthalten alle Pseudo- oder Paraplankter, die — auf dem Detritus wachsend — nicht zur echten Planktonfauna und -flora gehören. Durch weitere Methoden ist es nun noch möglich, den Detritus in anorganischen und organischen zu trennen: wenn man nach dem eingangs beschriebenen Verfahren auf chemischem Wege den Detritus ermittelt hat, so kann man diesen Gesamtdetritus unterteilen in anorganischen und organischen, indem man den Glühverlust des Sestons bestimmt und aus diesem Glühverlust auf die gesamte organische Substanz schließt. Von dieser gesamten organischen Substanz wird dann der Wert für das Phytoplankton und der Wert für das Zooplankton abgezogen. Der Rest entfällt dann auf den organischen Detritus. Selbstverständlich sind diese gravimetrisch-chemischen Methoden verhältnismäßig grob. Sie geben uns jedoch zur Zeit das einzige Mittel, um die mikroskopisch ermittelten Werte zu kontrollieren. Es empfiehlt sich in jedem Falle, beide Methoden, also die mikroskopische und die gravimetrisch-chemische, nebeneinander zu verwenden. Welche Methode den Vorzug hat, läßt sich nicht generell sagen, da dieses ganz von den örtlichen Gegebenheiten bestimmt wird, zum Beispiel von den Beimischungen von Feinsanden, wie sie besonders nach schwerem Wetter im Pelagial der Küsten auftreten.

Eine erste quantitative Darstellung des Detritus haben ARMSTRONG und HARVEY (1950) aufgrund ihrer Phosphoranalysen versucht. Diese Analysen geben ihnen über den Weg der Bestimmung des Gesamtphosphors, des gelösten anorganischen Phospors, des gelösten organischen Phosphors und des partikulären Phosphors zusammen mit mikroskopischen Beobachtungen Werte für den im Detritus festgelegten Phosphor. Dieser letztere erreicht nach HARVEY's Diagramm im Sommer sein Maximum. Dieses Diagramm ist jedoch als Schema zu betrachten, das uns überhaupt einen ersten Anhalt für die Relationen der einzelnen Phosphorkomponenten gibt.

3. Die Menge des Detritus in verschiedenen Meeresgebieten

Zunächst sollen einmal Angaben gemacht werden über die Menge des Detritus im hohen Ozean, wie wir sie aus Untersuchungen von HAGMEIER (1960) kennengelernt haben. HAGMEIER hat sich der gravimetrisch-chemischen Bestimmungsmethode bedient, das heißt also, er hat aus der Differenzbildung von Seston und den mikroskopisch ermittelten Werten für das Gewicht von Phytoplankton und Zooplankton den Detritus ermittelt. Wir wählen aus dieser Untersuchung einige signifikante Beispiele: in der Tabelle 2a geben wir zunächst einige Mittelwerte aus dem Oberflächenwasser des Seegebietes um Island. HAGMEIER hat dort im Mai-Juni 1953 gearbeitet und hat beispielsweise westlich Island — jedoch außerhalb des isländischen Küstenstromes — folgende bemerkenswerten Zahlen gefunden: bei einem Sestongehalt von 1·5 mg/l konnte er im Mittel aus 23 Proben einen Detritusgehalt von 57% berechnen. Die weiteren Mittelwerte aus dem Seegebiet um Island weisen recht unterschiedliche Detritusanteile bei Sestongewichten zwischen 0·2 und max. 1·5 mg auf. Im Extremfall liegen 96% von diesem als Detritus vor, wobei wir bedenken müssen, daß im Mai-Juni in diesem Gebiet noch eine Frühjahrsblüte herrschen kann.

Im Gebiet zwischen Island und den Orkneys konnte HAGMEIER an 32 Oberflächenproben einen Mittelwert von 0·45 mg Seston/l feststellen und fand auch nicht mehr als 27% Plankton, das heißt, daß auch hier weitaus der größte Teil des Materials aus Detritus bestand.

Aus der Tabelle 2b können wir Angaben über die Tiefenverteilung des Detritus entnehmen. So hat HAGMEIER zum Beispiel auf dem Reykjanes-Rücken Untersuchungen bis zu 650 m angestellt und dabei an der Oberfläche hohe

Tabelle 2

Menge und Zusammensetzung des Sestons im Seegebiet um Island
(HAGMEIER, 1960)

a. Oberflächenwerte Mai-Juni 1953 (HAGMEIER)

Seston mg/l	1·5	1·4	0·8	0·8	0·2	0·7	0·7
% Phytoplankton	41	54	4	10	4	4	1
% Zooplankton	2	2	2	3	1	5	3
% Detritus	57	44	94	87	5	91	96
Probenzahl	23	17	39	5	6	9	7

b. Tiefenverteilung des Sestons

Tiefe (m)	mg/l Seston	% Phytoplankton	% Zooplankton	% Detritus
		Reykjanes-Rücken		
0–50	1·5	39	0·1	61
150	0·3	5	0	95
350–450	0·1	17	0	83
650	0·1	1	0·2	99
		NW-Island		
0–10	2·4	59	0·3	41
120	0·7	0	0	100
220	0·9	1	0	99
320	0·6	1	0	99
420	1·3	0·1	0	100

Tabelle 3

Menge und Zusammensetzung des Sestons in der mittleren Nordsee, August 1953 (HAGMEIER, 1960)

a. Station 70 (58° 01′ N, 6° 44′ E) vor der norwegischen Küste

Tiefe (m)	0	10	20	30	40	50	60
Seston mg/l	0·6	0·5	0·4	0·1	0·5	0·4	0·4
% Plankton	11	17	12	78	10	4	1
% Detritus	89	83	88	22	90	96	99

b. Station 37 (Fladengrund, 57° 51′ N, 1° 26′ E)

Seston mg/l	0·6	0·7	–	4·7–2·0	0·7	0·5	–
% Plankton	3	2	–	38–48	9	3	–
% Detritus	97	98	–	62–52	91	97	–

Sestonwerte mit 1·5 mg gefunden, die einen Detritusgehalt von 61% aufwiesen. Je weiter man nun in die Tiefe kommt, desto geringer wird der Sestongehalt und um so höher wird der Detritusgehalt. Das bedeutet also, daß das Phytoplankton, das an der Oberfläche bei weitem den größten Anteil ausmachte, sehr schnell aufgezehrt wird oder noch nicht in diese Tiefen abgesunken ist. Auf einer Station im Nordwesten Islands finden wir um dieselbe Zeit ähnliche Verhältnisse. In der unmittelbaren Deckschicht von 0–10 m bestimmte HAGMEIER 2·4 mg Seston mit einem Detritusgehalt von 41%; 59% des Sestons bestanden aus Phytoplankton. In den größeren Tiefen sank der Sestongehalt auf 0·7, beziehungsweise 0·9 und 0·6 mg ab, wobei der Gehalt an Phytoplankton sehr schnell abnahm und in 420 m nur noch 0·1% betrug; der Detritusgehalt stieg dementsprechend auf 99–100%. Dieser hohe Anteil an Detritus ist um so bemerkenswerter, als es sich im Seegebiet um Island um reines atlantisches Wasser handelt, bei dem man eine Beimischung von Küstenwasser, beziehungsweise von Bodenwasser, in größerem Maße kaum erwarten darf. Der hohe Detritusgehalt ist hier nur durch einige wenige Beispiele belegt, ist aber von HAGMEIER durch vielfache Beobachtungen festgestellt worden. Leider liegen keine parallelen Untersuchungen über das größere Zooplankton vor, das als Produzent dieses Detritus in Betracht käme.

Man wird erwarten dürfen, daß mit der Annäherung an die Küsten diese Verhältnisse noch extremer werden. Aus einer anderen Untersuchung von HAGMEIER (1960) in der mittleren Nordsee im August 1953 (Tabelle 3a) nehmen wir zum Beispiel aus einer sestonarmen Station unweit der norwegischen Küste an der Oberfläche einen Sestongehalt von 0·6 mg mit einem Detritusgehalt von 89%, in 10 m Tiefe einen Sestongehalt von 0·5 mg mit 87% Detritus und in der Dichtesprungschicht in 30 m einen außerordentlich geringen Detritusgehalt mit 22% bei nur 0·1 mg Seston/l. Diese Tabelle wird ergänzt durch die Verhältnisse auf einer sestonreichen Station im Gebiet des Fladengrund (Tabelle 3 b), in der wiederum im Bereich der Dichtesprungschicht hohe Phytoplanktonwerte und entsprechend niedrigere Detrituswerte beobachtet werden, während im gesamten übrigen Wasserkörper der Detritus bei weitem die Menge des Planktons überwiegt, und zwar mit Werten von 91–98% Detritus im Seston.

Diese Ansammlung von Phytoplankton in der Sprungschicht wird durch eine Untersuchung von KREY (1954) in der mittleren Nordsee im Jahre 1952

Tabelle 4

Ansammlung des Detritus in der Sprungschicht

a. Mittlere Nordsee, August 1952 (KREY, 1954)

	Nördl. Doggerbank		Südl. Doggerbank		Extremwerte nördl. Doggerbank
Stationen	33	35	40	44	32
Tiefe der Sprungschicht, m	39	31	40	45	45
Phytoplankton-Gewicht mg/l	0·48	0·30	0·02	0·005	0·095
Seston mg/l	1·4	1·2	1·9	2·0	0·2
% Phytoplankton im Seston	34	25	1·1	0·25	49·4
% Detritus	66	75	99	98	51

b. Dauerstation 14/17 über der großen Fischerbank (August 1952)

(Mittelwerte aus jeweils 17 Proben)

Tiefen, m	20	25	30	35	40
Seston mg/l	0·28	0·27	0·27	0·54	0·25
Phytoplankton mg/l	0·2	0·5	2·2	5·8	7·4
% Phytoplankton im Seston	0·1	0·2	0·8	1·1	3·0
% Detritus	99·9	99·8	99·2	98·9	97·0
Extremwerte des Phytoplanktongehalts in %	0–0·7	0–1·3	0–13·0	0–4·9	0·6–17·1

bestätigt. Es wurden in der Dichtesprungschicht, die hier mit der Temperatursprungschicht identisch ist, max. 49·4% Phytoplankton gefunden und entsprechend ein Detritusgehalt von etwa 50%. Die Tabelle 4 a gibt Beispiele für die Verhältnisse in der Temperatursprungschicht sowohl für deren Tiefenlage als auch für die absolute Menge des Sestons, das in dieser gefunden wurde, als auch für das Phytoplanktongewicht, welches hier aufgrund der mikroskopischen Auszählungen bestimmt worden ist. Die Menge des Zooplanktons konnte nach der mikroskopischen Untersuchung der verhältnismäßig kleinen Proben vernachlässigt werden. Auch hier fällt auf, wie trotz dieser starken absoluten Ansammlung des Phytoplanktons doch ein sehr hoher Gehalt an Detritus festzustellen ist. Auf einer Dauerstation dieser Fahrt (Tabelle 4 b) über der großen Fischerbank wurde dem Verhältnis zwischen Seston und Phytoplankton in der Sprungschicht besondere Aufmerksamkeit gewidmet. In stündlichen Abständen wurden diese Werte aus den Tiefen 20, 25, 30, 35 und 40 m bestimmt. Die Sprungschicht lag zu dieser Zeit in etwa 35 m; dort wurde der höchste Sestongehalt mit 0·54 mg/l beobachtet und auch eine verhältnismäßig große Menge von Phytoplankton festgestellt. In jedem Fall betrug die Menge des Detritus über 80% der gesamten Sestonmenge. Das Detritusgewicht ist freilich wegen der geringen Sestonmenge verhältnismäßig niedrig.

Ähnlich hohe Detritusanteile wurden von KREY (1956) für das Gebiet der südlichen Nordsee beschrieben. In der Tabelle 5a werden Mittelwerte für das sogenannte Kanalwasser sowie für das englische Küstenwasser gegeben. Der Sestongehalt des Kanalwassers ist verhältnismäßig gering. Mit Hilfe der Eiweißreaktion, in diesem Falle also nicht mit mikroskopischen Untersuchungen, wurde die Menge der lebenden Substanz berechnet. Der Detritus liegt im Bereiche des Kanalwassers in einer Größenordnung von etwa 65%. Ganz anders zeigt sich das Bild im Bereich des englischen Küstenwassers, das sehr stark mit Seston beladen ist (4·95 mg/l). Die lebende Substanz ist zwar auch

Tabelle 5

Menge und Zusammensetzung des Sestons in der südlichen Nordsee (Mittelwerte in mg/L)

a. Südliche Nordsee, März 1952 (KREY, 1956)

	Kanalwasser	Englisches Küstenwasser
Seston	0·58	4·95
Lebende organische Substanz (Trockenwert)	0·205	0·38
Detritus	0·375	4·57
% Detritus in Seston	64·8	92·4

b. Dauerstation "Texel", März 1952 (HAGMEIER, 1960)

Mittlerer Sestongehalt	1·09
Mittelwerte Plankton	0·46 = 42·5 %
Mittelwerte Detritus	0·63 = 57·5 %

c. Seston und Detritus in der südlichen Nordsee, März 1953 (HAGMEIER, 1960)

	Hoofden		Doggerbank	
	Oberschicht	Unterschicht	Oberschicht	Unterschicht
Seston	1·94	3·98	0·78	0·90
Plankton	0·012	0·022	0·361	0·481
Detritus	1·93	0·396	0·41	0·42
% Detritus	>99	>99	54	47

	Austerngrund		Deutsche Bucht	
	Oberschicht	Unterschicht	Oberschicht	Unterschicht
Seston	0·69 –0·48	2·95 –1·24	1·66	2·01
Plankton	0·017–0·136	0·019–0·133	0·022	0·011
Detritus	0·67 –0·35	2·94 –1·11	1·64	2·00
% Detritus	72–98	89–>99	99	>99

hier höher als im Kanalwasser, erreicht aber proportional bei weitem nicht deren Anteil. So kommen wir hier zu einem Mittelwert für den Detritus von 92·4 %, was einer absoluten Menge von 4·57 mg/l entspricht.

Man sollte annehmen, daß der Detritusgehalt in Küstennähe infolge des vom Boden her beigemischten Materials erheblich ansteigen würde. HAGMEIER (1960) hat im März 1952 für eine Dauerstation bei Texel, auf der wiederum stündlich über 36 Stunden beobachtet wurde (Tabelle 5b), einen mittleren Sestongehalt von 1·09 mg/l ermittelt. Davon waren im Mittel 42·5 % planktischen Ursprungs, also 0·46 mg/l. Der Detritus betrug 57·5 %, das sind 0·63 mg/l. Wir finden also trotz der Küstennähe, die sich hier durch den starken Gezeitenstrom auswirken müßte, einen geringeren Wert für den Detritusanteil als in den früheren Beispielen.

In einer weiteren Tabelle (5c) sind die Seston- und Planktonwerte für Ober- und Unterschicht getrennt angegeben. So findet HAGMEIER für das Gebiet der Hoofden beispielsweise in der Oberschicht 1·94 mg Seston/l und in der Unterschicht 3·98 mg. Der Planktongehalt beider Schichten ist aber außerordentlich gering, sodaß wir in jedem Fall über 99 % Detritus beobachten. Im Gebiet der Doggerbank sieht es um dieselbe Zeit jedoch wesentlich anders aus: während in der Oberschicht 0·78 mg Seston und in der Unterschicht 0·90 mg bestimmt wurden, enthält das Wasser der Oberschicht 0·36 mg und das Wasser der Unterschicht 0·48 mg Plankton, das entspricht einem Detritusgehalt von 54 % beziehungsweise 47 %. Weitere Beispiele werden für

das Gebiet des Austerngrundes und für die Deutsche Bucht gegeben. Diese lassen einen wesentlich höheren Detritusgehalt erkennen, der zwar von Station zu Station erheblich schwankt, aber im wesentlichen doch nicht jene geringen Werte wie die auf der Doggerbank festgestellten erreicht. Die Doggerbank stellt also zu dieser Zeit ein Gebiet dar, wo durch die Frühjahrsblüte der Anteil des Detritus stark herabgedrückt ist. Absolut genommen sind aber auch in diesem Gebiet immer noch erhebliche Mengen von Detritus vorhanden.

Man könnte annehmen, daß auf diesen eben geschilderten Fahrten vielleicht besondere Verhältnisse angetroffen wurden. Nun hat BANSE (1956) im März 1955 (Tabelle 6) auf zwei Fahrten mit der "Anton Dohrn", wiederum Beobachtungen zu diesem Thema gemacht und gefunden, daß in einem Teilgebiet im Mittel 1·16 mg Seston vorhanden waren bei einem außerordentlich geringen Gehalt von lebender organischer Substanz von 0·04 mg, was einem Detritusgehalt von 96·6% entspricht. Nach Auslassung extremer Werte errechnete er als Mittelwert 0·98 mg Seston bei einem ähnlich niedrigen Wert für die organische Substanz von 0·039 mg/l, das einen Detritusgehalt von 96% ergibt.

Die vorher dargestellten Befunde aus dem Jahre 1952 und 1953 stehen also nicht vereinzelt dar, wenn die Frühjahrsblüte noch nicht eingesetzt hat.

Nach einer Untersuchung von POSTMA (1954) in der Nordsee unmittelbar vor dem holländischen Küstengebiet (Tabelle 7) bei Den Helder und in der holländischen Waddenzee entnehmen wir, wie zu erwarten, sehr hohe Seston-Mittelwerte, die in der Nordsee 6·0 mg/l und in der Waddenzee als Mittelwert 18·0 mg ergeben. Der Gehalt dieses Sestons an lebender Substanz ist nur verhältnismäßig gering und zwar im ersten Falle 0·77 mg/l und im zweiten Fall 1·85 mg. Der Anteil der lebenden Substanz wurde hier durch Bestimmung des Phosphors in der organischen Substanz ermittelt. Wir können also auch in diesem Gebiet mit einem hohen Detritusgehalt von 87% beziehungsweise 89·7% rechnen, was angesichts der außerordentlich starken Gezeitenströmungen nicht weiter verwunderlich scheint. Es bleibt jedoch dahingestellt, wieweit dieser Detritus nun organischen bzw. anorganischen Ursprungs ist. POSTMA analysierte für die Nordsee vor Den Helder 0·83 mg, für die Waddenzee 0·75 mg organischen Detritus, für den anorganischen Detritus 0·40 bzw. 15·40 mg/l. Es ist sehr wahrscheinlich, daß in einem Gebiet mit geringem vertikalen Dichtegradienten durch die Strömungen in unmittelbarer Küstennähe viel Detritus vom Boden ins freie Wasser gelangt.

Um den Effekt des Sediment-Detritus auszuschalten, ziehen wir die stark dichtegeschichtete Ostsee zum Vergleich heran, in der unter anderem GILLBRICHT (1951) 1949–50 auf dem Feuerschiff "Flensburg" Untersuchungen über den Gehalt an Seston und dessen Zusammensetzung angestellt hat. Er analysierte den Planktongehalt nach einer mikroskopischen Methode. Aus dieser Arbeit von GILLBRICHT (Tabelle 8a) entnehmen wir Mittelwerte z.B. für Oktober 1949 von 0·93 mg Seston/l mit einem Detritusgehalt von 92·4% und im März 1950 einen Sestongehalt von 1·19 mg/l mit einem Detritusgehalt von 91.8%. Gerade dieser letzte Befund erstaunt sehr, weil im März 1950 die Frühjahrsblüte des Phytoplanktons schon begonnen hatte und die Phytoplanktonmenge mit 0·09 mg/l nicht unbeträchtlich war. Nehmen wir den jahreszeitlichen Vergleich, den GILLBRICHT angestellt hat, dazu: in Tabelle 8 b finden wir im Bereich des Planktonmaximums in der gesamten Wassersäule einen Maximal-Wert von 12·8% Plankton im August und 19·1% im Oktober.

Tabelle 6

Menge und Zusammensetzung des Sestons in der südlichen Nordsee, März 1955 (BANSE, 1956)

(Mittelwerte für Oberflächenwasser in mg/l)

Proben	Zahl der Proben	Chlorophyll	Organische Substanz des Phytoplanktons	Trockensubstanz des Phytoplanktons	Eiweiß gesamt	Eiweiß des Phytopl.	Eiweiß des Zooplanktons
A	27	0·30	7·5	11	21·7	2·5	19·2
B	24	0·31	7·7	12	21·6	2·6	18·0

Proben	Organische Substanz = Trockensubstanz des Zooplanktons	Gesamtplankton (Bioseston)	Seston	% Bioseston im Seston	% Phytoplankton im Seston	% Detritus im Seston
A	29	40	1160	3·4	1·0	96·6
B	27	39	980	4·0	1·2	96·0

Tabelle 7

Menge und Zusammensetzung des Sestons im holländischen Küstenbereich (POSTMA, 1954), Mittelwerte

	Nordsee vor Den Helder	Waddenzee	Malzwin	
Seston mg/l	6·0	18·0	39·6	
OS (Gl)*	1·50	2·50	7·95	
OS (P)*	0·77	1·85	1·83	OS (EW)
Detritus (gesamt)	5·23	16·15	37·77	
Detritus (organisch)	0·83	0·75	6·12	
Detritus (anorganisch)	4·40	15·40	29·82	
% Detritus im Seston	87·0	89·7	95·2	

*OS: organische Substanz.
(Gl) aus dem Glühverlust ermittelt.
(P) lebende OS aus dem partikulären Phosphor berechnet.
(EW) aus Eiweißanalysen berechnet.

Tabelle 8

Menge und Zusammensetzung des Sestons in der Kieler Bucht

(Mittelwerte nach GILLBRICHT (1951) auf FS "Flensburg" 1949–1950 in mg/l)

a.	Oktober 1949	März 1950
Seston	0·931	1·192
Chlorophyllhaltiges Seston	0·151	0·342
Phytoplankton	0·069	0·088
Clorophyllhaltiger Detritus	0·082	0·254
Chlorophyllfreier Detritus	0·780	0·850
Gesamt-Detritus	0·862 = 92·4 %	1·094 = 91·8 % von Seston

% Plankton im Seston

b.	1949			1950		
Monat	Juni	August	Oktober	Januar	März	Juni
Im Bereich des Planktonmaximums	1·1	12·8	19·1	0·4	24·9	11·4
Gesamte Wassersäule	0·8	4·7	8·0	0·3	6·9	1·2
Mittlerer Detritusgehalt (%) der gesamten Wassersäule (28 m)	99·2	95·3	92·0	99·7	93·1	98·8

Tabelle 9

Menge und Zusammensetzung des Sestons in der mittleren Ostsee
(BANSE, 1957)

	Mittelwerte für Seston mg/l	leb. organ. Subst. mg/l	% leb. Substanz im Seston	% Detritus im Seston
Warme Deckschicht	0·24	0·065	27	73
Sprungschicht	0·40	0·067	16·8	83·2
Kalte Zwischenschicht	0·12	0·029	24	76
Bodenschicht	0·22	0·021	9·5	90·5

Die Werte von GILLBRICHT, die von BANSE (1956) kritisiert worden sind, ergeben für die gesamte Wassersäule, also unter Einrechnung des Bereichs des Planktonmaximums, für alle Monate einen erstaunlich hohen Gehalt des Wassers an Detritus. Dieser ist im Oktober am geringsten, wahrscheinlich infolge der starken Wirkung der Dinoflagellatenblüte.

Man kann vermuten, daß die Untersuchungsergebnisse von GILLBRICHT auf dem FS "Flensburg" unter zu starker Landnähe gelitten hätten. Wenn wir nun aus der Landnähe in die landfernen Gebiete der mittleren Ostsee rücken, wo sowohl durch den Salzgehalt als auch durch eine starke Vertikalschichtung die Temperatur bedingt ist, ein Beispiel von BANSE (1956) aus dem Jahre 1956 aufgreifen, so beobachten wir trotz einer extrem starken Dichteschichtung in allen untersuchten Wasserkörpern des Gotland- und Bornholmbeckens hohe Detrituswerte. In der Tabelle 9 unterscheidet BANSE zwischen einer warmen Deckschicht, einer Sprungschicht, in der wir besonders hohe Sestonwerte erwarten können, einer kalten Zwischenschicht, die sich aus dem Winterwasser herleitet und der Bodenschicht. Er hat das Seston mit chemischen Methoden in seine Bestandteile gegliedert und dabei für die warme Deckschicht einen Betrag von 73% Detritus bestimmt, eine immerhin noch erstaunliche Menge, wenn man die hydrographischen Bedingungen in Betracht zieht. Daß der Detritus nach dem Boden zu größere Werte annimmt, erscheint weiter nicht verwunderlich, da mit zunehmender Tiefe der Anteil des Phytoplanktons abnimmt.

Zur Ergänzung der Beispiele aus der Ostsee, insbesondere der von GILLBRICHT aus der westlichen Kieler Bucht, seien zwei Diagramme gebracht, die die Vertikalverteilung des Detritus auf einer Station in der Kieler Bucht bei Boknis Eck zeigen. Dieses Beispiel ist methodisch besonders bemerkenswert, weil die Menge des Detritus und die des Phytoplanktons hier erstmalig anhand einer Mikrophotographie mit dem Teilchengrößen-Analysator bestimmt worden sind. Unterziehen wir zunächst einmal die zahlenmäßige Verteilung der einzelnen Partikelgrößen in den sechs verschiedenen Tiefen einer näheren Betrachtung (Fig. 1):

Es zeigt sich klar, daß in allen Tiefen die feinste, hier beobachtete Fraktion (3·85 µ Durchmesser) weitaus am stärksten vertreten ist. Sie nimmt von der Oberfläche bis zum 10 m-Horizont von 610,000 auf 167,000 Teilchen pro Liter ab und steigt dann nach der Tiefe zu wieder an. Der Extremwert dieser kleinsten Größenklasse wird in dem hydrographisch besonders gekennzeichneten Bodenwasser mit über 1,152,000 erreicht. Die hohe Anzahl der kleinsten Partikel an der Oberfläche kann durch deren geringe Sinkgeschwindigkeit erklärt werden, der extrem hohe Wert in der Bodenschicht durch aufgewir-

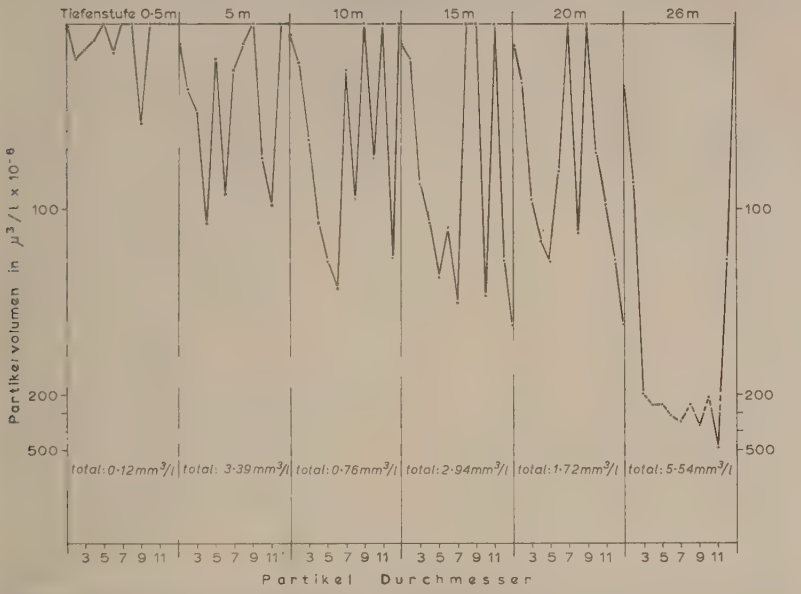

Figure 1. Number of detritus particles, in thousands per litre at different depths at the station Boknis Eck, 8. November 1960.

Abscissa: particle size in groups. Mean diameter of groups in μ: —

1 = 3·85	6 = 23·10	10 = 38·50	Total = total numbers of all
2 = 7·70	7 = 26·95	11 = 42·35	particles within the range
3 = 11·85	8 = 30·80	12 = 46·30	3·85 — 119·35 μ diameter.
4 = 15·40	9 = 34·65	13 = 50·05	
5 = 19·25			

belten — also nach der eingangs gegebenen Definition allochthonen Detritus. Die Unterschiede in der Mengenverteilung der übrigen Korngrößen sind bei weitem nicht derart groß: Das Minimum der Partikel mit einem mittleren Durchmesser von 7·7 μ befindet sich in 15 m, was wegen des mit steigender Größe geringer werdenden Reibungswiderstandes zu erwarten ist. Alle weiteren Größenklassen haben ihr Minimum an der Oberfläche, wenn man von einigen ausschließlich statisch bedingten Unregelmäßigkeiten absieht. Die großen Detrituspartikel mit einem mittleren Durchmesser von $>$ 20 μ sind mit Werten zwischen 10 und 20,000 Teilchen/l annähernd gleichmäßig in der Wassersäule verteilt, wenn man von einer strömungsbedingten Anreicherung bis zu 60,000/l im Bodenwasser absieht. Die Detrituspartikel von 50 μ Durchmesser werden hier wegen ihrer geringen Anzahl und der damit verbundenen statistischen Unsicherheit in der methodischen Erfassung nicht näher dargestellt.

Rechnet man nun die Volumina der einzelnen Größenklassen nach der Kugelformel aus, dann verschiebt sich das Verteilungsbild gegenüber der Verteilung der Anzahl völlig. Für biologische Betrachtungen, insbesondere solche über Nahrungsfragen, sind die Detritusvolumina oder -gewichte jedoch weitaus wichtiger als die Anzahl der Detrituspartikel, die andererseits für meeresoptische Fragen von größerem Interesse sind. Fig. 2 läßt deutlich er-

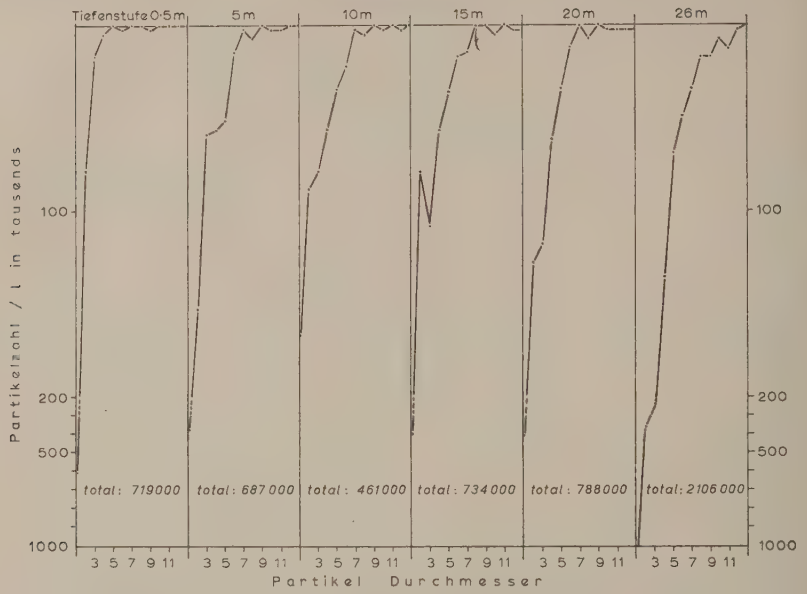

Figure 2. Volume of detritus per litre at different depths at the station Boknis Eck, 8. November 1960. Details of diameters as in Figure 1.

kennen, daß die Volumina der kleinsten, hier beobachteten Partikel (bis etwa 10 µ) nur eine sehr geringe Rolle im Gesamtbestand spielen. Schon die Partikel mit einem mittleren Durchmesser von 15·4 µ nehmen in den mittleren Tiefenhorizonten einen beträchtlichen Anteil am Gesamtvolumen ein. An der Oberfläche (0·5 m) sind sie nur spärlich vertreten, im Bodenwasser (26 m) hingegen in großer Menge. Die Partikelklassen zwischen 19·25 und 34·65 µ weisen fast immer die relativ größten Massen in dem gesamten, hier abgebildeten Spektrum auf. In der Gesamtaufnahme, die sich bis zu Partikeln von einem Durchmesser bis 119·35 µ erstreckt, fallen jedoch vereinzelt vorkommende große Partikel stark ins Gewicht bei der Berechnung des Gesamtvolumens. Stärkere Schwankungen finden eine statistische Erklärung. Es wird einer eingehenden Untersuchung in verschiedenen Meeresgebieten und -tiefen sowie zu verschiedenen Zeiten bedürfen, um hier allgemeingültige Aussagen machen zu können.

In Tabelle 10 sind die Werte für die Gesamt-Volumina des Detritus und des Phytoplanktons zusammengefaßt. Die Werte für den Detritus bewegen sich zwischen 0·12 mm^3/l für die Oberfläche und 5·54 mm^3 für das Bodenwasser und lassen in den Zwischentiefen keine Tendenz erkennen. Dagegen nimmt das Volumen des Phytoplanktons von der Oberfläche mit 0·77 mm^3 bis zur Grenze der Deckschicht, die in 20 m liegt, mit kleinen Unregelmäßigkeiten bis auf 2·10 mm^3/l zu.

Eine Umrechnung der Volumenwerte des Detritus in Gewichtseinheiten kann heute nur mit geschätzten Faktoren erfolgen. Wir dürfen dabei von der Überlegung ausgehen, daß der Detritus — ohne seinen Bakterienbewuchs —

Tabelle 10

Detritus und Phytoplankton auf Station Boknis Eck (Kieler Bucht) am 8. November 1960

Tiefe m	Detritus Volumen mm³/l	Detritus Gewicht mg/l	Phytoplankton Volumen mm³/l	Phytoplankton Gewicht mg/l	Gesamtgewicht mg/l	% Detritus am Gesamtgewicht
0·5	0·12	0·05	0·77	0·19	0·24	21
5	3·39	1·36	1·48	0·37	1·73	79
10	0·76	0·30	1·10	0·28	0·58	52
15	2·94	1·18	1·96	0·49	1·67	71
20	1·72	0·69	2·10	0·53	1·22	57
26	5·54	2·22	0·02	0·01	2·23	96

Das Bodenwasser erweist sich als außerordentlich arm an Phytoplankton.

aus zerfallener, lebender Substanz besteht, bei der zumindest der Lebensträger Eiweiß durch Wasserabgabe stark denaturiert ist, wenn er nicht — wie in den meisten Fällen — völlig zerfallen ist. Man muß also einen wesentlich höheren Anteil der Trockensubstanz am Volumen ansetzen als bei den Ausgangsstadien. Für diese gibt HAGMEIER (1961) Mittelwerte zwischen 17 und 27% des Volumens der verschiedenen Organismenklassen an. Wir entfernen uns wohl nicht zu weit vom wahren Mittelwert, wenn wir etwa 40% des Volumens des Detritus als Trockensubstanz für die weiteren Rechnungen ansetzen. Dabei bleibt zunächst die Frage nach dem spezifischen Gewicht noch offen. Wir haben es also in den Gewichtsangaben für den Detritus in Tabelle 10 mit einem Wert zu tun, der gegenüber den Gewichten des Phytoplanktons relativ unsicher ist, zumal wir über seinen anorganischen Anteil nichts wissen.

Die Vertikalverteilung des Gewichts von Detritus und von Phytoplankton zeigt naturgemäß dieselben Grundzüge wie die des Volumens. Erst das Gesamtgewicht beider ergibt ein anderes Bild, welches in seiner Tendenz vom Detritusgewicht bestimmt wird. Der Gesamtwert für das Bodenwasser mit 2·23 mg/l hält sich jedoch in der Größe der Werte in 5 und in 15 m.

Für unsere Fragestellung nach dem prozentualen Anteil des Detritus gibt die letzte Spalte der Tabelle 10 eine Bestätigung der früher mit völlig anderen Methoden gefundenen Werte. Der Detritusanteil an der Gesamtsubstanz hält sich zwischen 21% und 96% am Boden. Der sehr niedrige Gewichtsanteil an der Oberfläche steht in Zusammenhang mit der Sedimentation der hier an Zahl zurücktretenden größeren Partikel. Der sehr hohe Detritusanteil am Boden kann nur durch strömungsbedingte Aufwirbelung von Bodenmaterial erklärt werden. Der Mittelwert für den Detritusgehalt steht mit 62% im Rahmen dessen, was mit anderen Analysenmethoden gefunden wurde.

Es dürfte nun besonders reizvoll sein, den Anteil des Detritus im Pelagial des Süßwassers zu untersuchen. Wir verfügen da über eine ausgezeichnete Arbeit von DAVIS (1958) aus dem Lake Erie vom Jahre 1956, wo er von Juni bis August den Gehalt dieses Sees an Phytoplankton, Zooplankton, organischem und anorganischem Detritus auf rein mikroskopischem Wege bestimmte. Aus 21 Proben hat er einen Durchschnittswert von 31·95 mm³ Seston/l berechnet, davon waren 19·00 mm³ Phytoplankton, 4·7 mm³ Zooplankton, 7·8 mm³ organischer Detritus und 0·45 mm³ anorganischer Detritus. Demnach nimmt der Detritus hier nur 26% der Gesamtmenge des Sestons ein, das hier zwar nur als Volumen angegeben wird. Eine Arbeit von BURSCHE (1959)

Tabelle 11

Die Zusammensetzung des Sestons in der Elbmündung
(BURSCHE, KÜHL und MANN (1958)), Einzelwerte in mg/l, 11.–12. Mai 1956

	Seston	Organische Substanz	EW=leb. Subst.*		% Detritus
Blankenese (km 635)	15·5	5·5	4·15 ≈	8·3	46
Glückstadt (km 675)	16·3	4·0	1·56	3·12	80
Schellenkuhle (km 685)	23·4	5·6	1·38	2·76	91·5
Brunsbüttel (km 700)	55·0	8·7	1·60	3·20	94·2
Otterndorf (km 710)	22·5	4·6	0·40	0·80	96·4
Cuxhaven (km 724)	8·9	0·7	0·33	0·66	92·6
Feuerschiff "Elbe 3"	15·9	–	0·85	1·70	89·3
Feuerschiff "Elbe 2"	10·6	6·1	0·85	1·70	84·0

*) EW = Eiweiß.
leb. Subst. = lebende Substanz (Trockengewicht).

unterstützt die eben genannte Arbeit, obwohl die Untersuchungen von BURSCHE in den verhältnismäßig sehr kleinen Seen im Kreise von Berlin unternommen wurden im Gegensatz zu dem Lake Erie, der mit seinen außerordentlich großen Dimensionen der Kieler Bucht zu vergleichen ist. BURSCHE kommt zu dem Ergebnis, daß von 46 Wasserproben nur 6 einen Detritusgehalt von über 15% des Gesamtsestons aufwiesen. Von diesen 46 Proben zeigten sogar 19 einen Detritusgehalt von unter 5% des Sestons. BURSCHE hat ihre Untersuchungen auf mikroskopischem Wege durchgeführt. Wenn wir einen Übergang zwischen dem Süßwasser und dem Meere suchen, so finden wir in einer Arbeit von BURSCHE, KÜHL und MANN (1958) in der Elbmündung ein willkommenes Beispiel. In Tabelle 11 sind einige ihrer Hauptwerte wiedergegeben. In der Zeit erhöhter Planktonproduktion, im Mai 1956 beispielsweise, finden wir im reinen Elbwasser bei Blankenese schon 46% Detritus. Der Anteil steigt bis Otterndorf, wo wir etwa 96·4% Detritus bei einem Gesamtsestongehalt von 22·5 mg/l finden.

Von da ab bis zum Feuerschiff "Elbe 2" sinkt der Detritusgehalt wieder bis auf 84% bei einem Sestongehalt von 10·6 mg/l. Es zeigt sich also auch hier, daß im Süßwasser wesentlich weniger Detritus vorhanden ist als in vergleichbaren Meeresgebieten. Selbstverständlich ist dieser Abschnitt der Elbe, in dem starke Gezeitenströmungen herrschen, als eine besondere Ausnahme zu betrachten. Immerhin ist gegenüber der freien Nordsee der relative Detritusgehalt trotz des erhöhten Sestongehaltes hier nicht wesentlich verändert. Es wird einer besonderen Untersuchung bedürfen, auf welchen Vorgängen diese Verhältnisse beruhen. Vermutlich werden die Bakterien in dieser Rechnung eine sehr starke Rolle spielen.

Wenn wir jetzt die Verhältnisse im gesamten Meere überschauen, soweit uns bislang Beispiele vorliegen, so können wir feststellen, daß stets ein hoher Betrag an Detritus vorhanden ist, der meistens den des Planktons um ein Vielfaches übersteigt und nur in wenigen Fällen bis auf die Größe des Planktonanteils absinkt. Es bleibt die Frage, wie dieses überraschende Mengenverhältnis zu deuten ist. Die Erklärung liegt nahe, daß das Phytoplankton von den größeren Zooplanktern, die mit den hier angewandten Methoden nicht erfaßt werden können, wie zum Beispiel den größeren Copepoden, den Salpen oder den Pteropoden usw. verhältnismäßig schnell gefressen wird, sodaß es gegenüber

dem durch diese Zehrungsvorgänge gebildeten Detritus in einen verhältnismäßig geringen Anteil herabgedrückt wird. In Zukunft wird es zur Klärung dieser Verhältnisse nötig sein, auch die größeren Plankter quantitativ zu erfassen und Untersuchungen über deren Nahrungsverwertung anzustellen.

An den hier gegebenen Beispielen zeigt sich, daß der Detritus im Meere eine außerordentlich bedeutsame Rolle spielt. Die Untersuchungen von BARKER JØRGENSEN (1955) zeigen uns, daß ein Mindestmaß von geformter organischer Substanz im Wasser vorhanden sein muß, um überhaupt die Existenz der Filtrierer zu ermöglichen. Aus seiner zusammenfassenden Arbeit kann man entnehmen, daß die planktischen Copepoden als Mittelwert 0·8 mg geformte und verwertbare organische Substanz im Liter Wasser benötigen, damit allein der Energieaufwand, der für die Filtration notwendig ist, gedeckt wird.

Leider wissen wir noch allzu wenig über die Verteilung des Detritus im hohen Ozean, wie auch besonders in der Tiefsee. Es ist wahrscheinlich, daß durch die Arbeiten im IGY auf den Forschungsschiffen "Gauss" und "Anton Dohrn" ein Beitrag zur Klärung dieser Fragen erzielt wird. Dieses ist um so notwendiger, als sich immer mehr die Frage aufdrängt, wovon die zahlreichen Tiere in tieferen Wasserschichten und in der Tiefsee leben. Selbstverständlich bietet sich uns der unmittelbare, aktive Transport von lebender organischer Substanz durch die Vertikalwanderung von Zooplanktern an. Wir müssen aber auch für die zahlreichen Detritusfresser, die in großen Tiefen leben, nach einer ausreichenden Nahrungsquelle suchen. Die Arbeiten in den kommenden Jahren werden uns auch auf diesem Gebiet weiterführen, zumal durch neuere Methoden ein Fortschritt und eine Erleichterung in der Bearbeitung des gesammelten Materials möglich wird.

4. Summary

1. This review shows the important part that detritus plays in the nutrient cycle and particularly its role in the nutrition of the filter-feeders. An amount is given of the different methods now available for its quantitative analysis.

2. In the past 10 years a number of authors have collected quantitative data on the abundance of detritus in the open sea and coastal waters. In Icelandic waters and in the North Sea detritus has been found to make up 40–90% or more of the seston weight, even during the peak of phytoplankton production. The percentage of detritus is rarely below these values.

3. In the coastal areas of the North Sea and the Kiel Bight, POSTMA (1954) and GILLBRICHT (1951) have shown that the proportion of detritus present is always 90% or more. This is due to tidal currents and upwelling which take the detritus from the bottom into midwater

4. In the central Baltic BANSE (1957) found high percentages of detritus (73–90%) although a marked discontinuity layer was present.

5. A short account is given of a new quantitative method of analysing detritus. Using the Zeiss particle-size-counter and microphotographic techniques the total number and size of living and dead particles in a sample can be determined. Using plankton-equivalent factors, the weight of the total dry substance and the proportion of detritus can be calculated. With this visual method high percentages of detritus were found (52–96%), except in surface samples, where the proportion of detritus was down to 21%.

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An Automatic Method of Counting Fish Echoes

By

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I. The Equipment (by R. B. Mitson)

1. Introduction

It has been shown that a relationship exists between visual counts of echo signals from fish close to the seabed, and fish catches for the periods of observation. In the Arctic, echo surveys have been made, using standard echo-sounders, to determine the presence and abundance of fish which were predominantly cod. A visual counting method was used, with operators counting signals from a calibrated cathode ray tube display. The results of this work have been described by Richardson, *et al.* (1959). The operators tired quickly with the visual counting system, and because amplitude levels could not be judged accurately information was continuously lost. It was therefore decided to design an electronic system of counting echoes, to the following specification: —

1. An amplitude range that could be set up to plus 30 db (i.e. 31·6 times) with respect to noise level.
2. To count only in the three fathoms (5·5 m) apparently above the seabed.
3. To reject seabed signals that are broken up by aeration, etc.
4. To count separately the number of good seabed echoes.

2. Method

(a) Principle

The expanded portion of the cathode ray tube display (Figure 1, (b) and (e)), showing the seven fathoms (12·8 m) above the seabed, is a convenient switch for an echo delay unit. In the delay unit the echoes are effectively

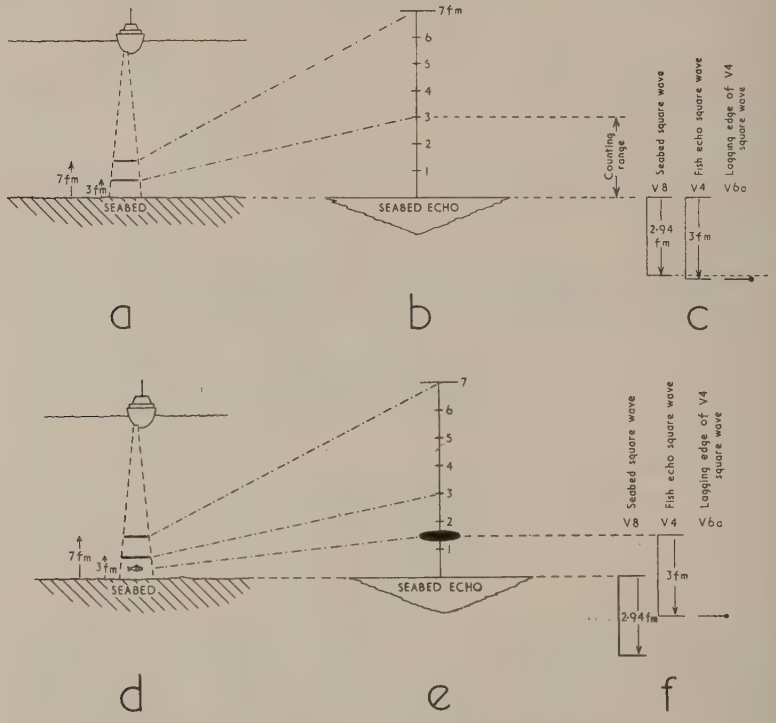

Figure 1. Diagram illustrating the sounding system.

(a) Ship sounding. No fish in counting range.
(b) Picture as seen on expanded display of a cathode ray tube.
(c) Relevant waveforms in echo delay unit drawn to scale.
(d) Fish 1½ fathoms off seabed.
(e) Expanded display of cathode ray tube showing fish at 1½ fathoms off seabed.
(f) Fish echo square wave now advanced in time due to fish echo. Lagging edge (V6 pulse) occurs during time of seabed pulse.

separated into fish and seabed echoes; this is because there are two circuits, one of greater sensitivity than the other. Thus if a fish echo occurs within the counting range of three fathoms (5·5 m) from the seabed, the timebase of the sensitive circuit will generate a square wave in response. Although the seabed echo will also be present a little later, it will produce no response from this circuit, for once the square wave has been initiated the circuit is effectively desensitised for the duration of that wave. If no fish echo is present within three apparent fathoms of the seabed, the seabed echo will start the square wave (see Figure 1 (c)). The less sensitive seabed square wave circuit "sees" the same sequence of echoes, but can only respond to the high amplitude of the seabed echo.

It is necessary to use the seabed echo as a reference for counting fish echoes at a pre-determined distance from it. Unfortunately, these echoes occur in time before the seabed echo, and so a time delay for the fish echo is necessary. A delay line may be used for this purpose, but is expensive to construct for the low frequencies used in echo-sounding, and in this case the duration of a square wave is used to provide a suitable delay.

It is shown in Figure 1 (c) that when no fish echo is present the square waves for both fish and seabed echoes start at the same point, the seabed, and by arranging that the square wave from the seabed echo is of slightly shorter duration than the fish echo square wave a fixed counting clearance from the seabed is obtained. This clearance is considerably less than the pulse length of the echo-sounder, i.e. 0·5 milliseconds.

When a fish echo is visible within the three fathoms above the seabed, as shown in Figure 1 (e), the fish echo square wave starts at the point of maximum amplitude of this echo, and as the square wave has a constant length of three fathoms (Figure 1 (f)), its lagging edge appears in time within the square wave started by the seabed echo. By causing the seabed square wave to hold a valve ready for conduction, the lagging edge of the fish echo square wave may be used to "open" this valve completely, and a count pulse passes through to the electromagnetic counter circuit.

(b) The 3 amplitude fish echo counter

(i) *Outline of system*

The system in regular use at the Lowestoft laboratory is shown in block diagram, Figure 2. It consists of a 30 kc/s paper recording echo-sounder (Kelvin Hughes MS 29), with a standard transducer which feeds signals to a cathode ray display unit. These signals are amplified in the usual manner, and an output is taken from one plate of the CRT and passed to three identical echo delay units. A square wave produced by the expanded timebase,

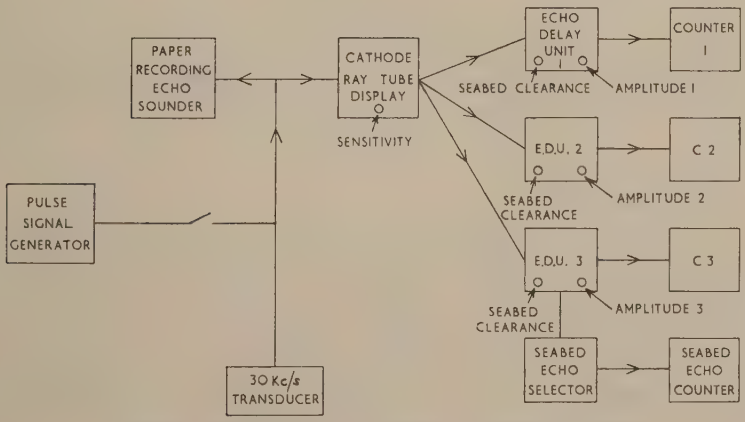

Figure 2. Block diagram of complete 3 amplitude system.

corresponding to seven fathoms depth, is also passed to the delay units; this square wave switches on the amplifier circuits in the echo delay units for the duration of seven fathoms only. In the system now in use the expanded timebase must be set manually over the seabed echo; an automatic tracking device is being developed to overcome this difficulty.

(ii) *Calibration and testing*

For testing and calibration a pulse signal generator is used to inject an imitation fish echo in series with the transducer, and consequently into the CRT display. This simulated fish echo is a 30 kc/s pulse which may be varied in length or in amplitude, and can be placed anywhere in time on the paper record or CRT display. The range of amplitude variation is from 10,000 microvolts to 0·1 microvolt in steps of 1 db (i.e. a voltage ratio of 1·22 times). Pulse length may be switched to 0·5, 1, 2, or 5 milliseconds, but it has been found that the 1 millisecond pulse is the most useful for setting up and calibrating the 3 amplitude counters.

(c) Method of setting up for counting

This is done whilst the ship is steaming and preferably when no true fish echoes are visible. The sensitivity of the CRT display unit amplifier is set in the normal manner, i.e. adjusted until maximum tolerable noise level is reached, then turned very slightly down from this level. The noise level is measured by reducing the amplitude of the injected pulse until it just disappears, and then it is increased by 1 db. It is now possible to read off the noise level from the amplitude scale on the pulse signal generator. It has been found that levels of 6 db, 12 db, and 18 db (i.e., 2, 4, and 8 times), above noise level are suitable for counting.

The seabed clearance controls are rotated until all counters are counting, then turned back 0·5 fathom (0·9 m) on the scale. Assuming that the simulated fish echo is placed within the counting range of three fathoms from the seabed, its amplitude may now be increased by 6 db over the noise level. This is the required level for the first counter to operate. By advancing the amplitude control on the first echo delay unit the corresponding counter will start, the point where it just commences counting being the correct level. This procedure is repeated for the other two units, which are set at their respective levels. The pulse generator is then switched off, counters set to zero and counting can start.

(d) Circuit description

There are two inputs to each echo delay unit, labelled "Signal" and "Gating pulse" respectively. The "Signal" circuit receives information on the whole water column from a few fathoms beneath the ship to the seabed. Into the "Gating" circuit comes a square wave of 7 fathoms effective scan from the expanded timebase of the CRT display, which is passed through a DC amplifier coupled to the cathode of the first valve amplifier, V1.

The valve V1 is a 30 kc/s tuned amplifier and it operates only for the period during which it is switched on by the "Gating pulse", i.e. a seven fathom "slice" of the water column. There are two outputs from the tuned transformer

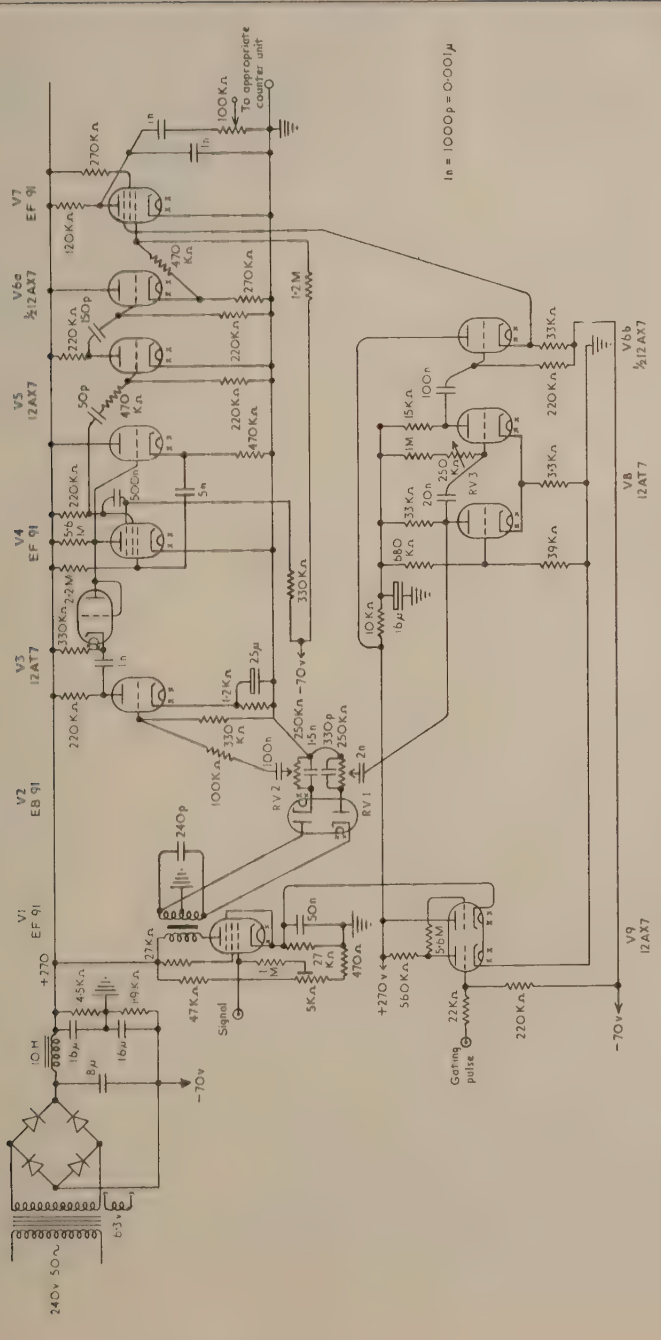

Figure 3. Circuit diagram of one of the three echo delay units.

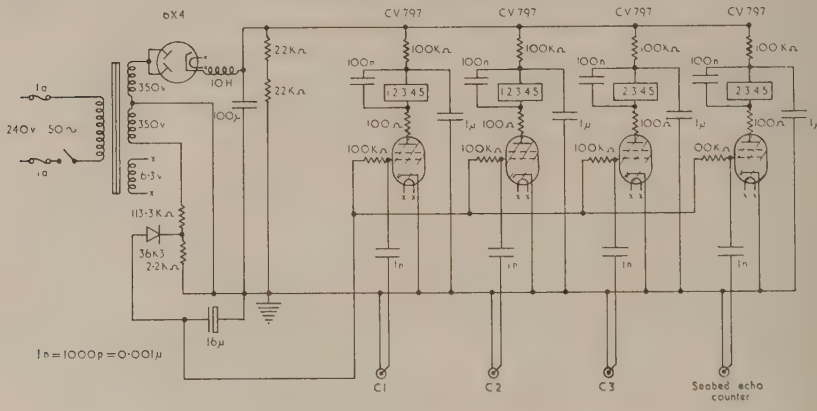

Figure 4. Counter unit circuit diagram.

in the V1 circuit (see Figure 3), the top circuit for small signals (i.e. fish) and the other which is triggered from the seabed signal.

A double diode valve, V2, rectifies the amplified signal. The negative signals, with respect to earth, trigger a cathode coupled flip-flop (the twin triode valve V8). It is arranged that the amplitude required to trigger this circuit is such that only the seabed signal can do so. The square wave output pulse from the valve V8 is of 6 to 9 milliseconds duration, which is varied by RV3, called the Seabed Clearance Control. This square wave duration corresponds to sound path lengths in sea water of from 4·9 fathoms (8·8 m, a depth in echo of 2·45 fathoms, 4·4 m), to 7·4 fathoms (13·4 m, a depth in echo of 3·7 fathoms, 6·7 m). The positive square wave output from valve V8 is fed through a cathode follower to the suppressor grid of pentode valve V7, a coincidence detector, normally cut off by a negative supply voltage.

Returning to V2a, it is seen that a positive signal (with respect to earth), is developed across RV2 which is the Fish Echo Amplitude Control. An output from the control is taken to V3 which provides sufficient amplification to trigger V4 from the smallest fish echo likely to be seen.

A transitron type of square wave generator, pentode valve V4, produces a pulse of fixed duration (7·3 milliseconds) corresponding to a sound path length in water of 6 fathoms (11 m, i.e. a depth in echo of 3 fathoms, 5·5 m). This is the effective counting range of the equipment. The square wave at the screen grid of V4 is differentiated and amplified, the portion of interest being the lagging edge of the square wave. At the cathode of V6a this lagging edge appears as a sharp single pulse of positive polarity, having sufficient amplitude to overcome the negative bias on the control grid of V7. Thus if the V7 suppressor is being held open at this period by the seabed square wave the single pulse will pass through to the appropriate counter circuit (Figure 4). Assuming this is C1 counter, the pulse will cause the thyratron in C1 circuit to fire and conduct heavily, discharging the 1/μF capacitor through the winding of the electromagnetic counter. The capacitor immediately begins to charge again ready for the next pulse.

(e) Errors and interference

During the early trials of this equipment large errors occurred in the counts, which were due to two main causes; they were:

(i) Electrical interference on the ship.

(ii) Bad weather conditions.

(i) *Electrical interference on the ship*

On several occasions electrical interference was severe at the extremes of the ship's roll, and a large number of high amplitude short length pulses were seen on the display CRT, probably due to "hull slapping" by masses of air bubbles. These pulses caused erratic triggering of the fish signal timebase, which counted all the interference pulses — perhaps as many as twenty during the period of only one transmission. The equipment was useless under such conditions of almost continual interference and this problem had to be tackled in two ways: —

(a) Reduction of electrical interference to a minimum.

(b) Arrangement of the system so that for each counter not more than one count could be registered in each transmission period. To realize this it was decided to use a small thyratron valve which on being triggered by the "count" pulse would conduct heavily and discharge a capacitor through the winding of an electromagnetic counter. The time constant is such that it is impossible for the counter to register again before the next transmission can take place.

(ii) *Bad weather conditions*

It has been found in practice that if the echo-sounder results can be interpreted by the eye, then in general the counting system can do so. At first it was considered necessary only to count the number of transmissions made by the echo-sounder, but in view of the large numbers of missing signals due to aeration under bad weather conditions it was found necessary to count the "good" returns of seabed echoes. A square wave taken from the cathode of V8 and passed to the seabed echo selector fulfills this requirement. Good returns of seabed echoes for the purpose of counting are those having an amplitude greater than a certain pre-determined value, but in some cases a broken-up seabed echo appears, reaching sufficient amplitude to open the coincidence detector only some long time after its initial edge appears. This edge appears as a pulse of variable amplitude, called an X echo (RICHARDSON, *et al.*, 1959), and is liable to be counted as a fish echo close to the seabed, if the seabed clearance control is not set sufficiently high.

3. Some Inherent Limitations of the System

1. Because a standard echo-sounder is used, with its relatively wide transducer beam (approximately thirty degrees laterally and twenty degrees fore and aft of the vessel, between half power points), a depth error does occur for fish swimming near the edge of the sound cone. Those fish swimming well above trawl headline height can appear to be much closer to the seabed than they

actually are, and their echoes will be counted by this system. Therefore, to reduce this source of error a narrow beam system is needed.

2. With a sharp decrease in depth of seabed, the water noise level may increase sufficiently to be counted by the most sensitive counter. Regular checks of noise level are therefore necessary when large changes of depth occur.

II. Trials with the Fish Counters (by R. J. Wood)

Introduction

The fish counter unit was tested between 20. to 23. July 1959 on the R.V. "Ernest Holt". Reliable fish counts were obtained on a total of 15 trawl hauls while fishing on the Bellsund and Hornsund Banks off the west coast of Spitsbergen. The bottom depth during these hauls varied between 43–68 fathoms (78·6–124·3 m) and catches ranges from 4¼–110 baskets. The capacity of a basket is 6 stones (38·1 kg), and it will hold between 15 and 17 cod of 70 cm length. The catches consisted predominantly of cod, with some haddock.

Method and Results

The fish counters were set up as described, after the general noise level had been measured. During this series of observations the general noise level was always in the region of 10 microvolts, and the 3 counters (C3, C2, and C1) were set to count signals at levels of 20, 40, and 80 microvolts respectively, i.e. 6 db, 12 db, and 18 db with respect to noise level of 10 microvolts. The procedure adopted during counting was for the counters to be read and reset to zero after every 1000 counts recorded by the seabed echo counter, i.e. transmissions from which a good seabed signal was received. The mean bottom depth during this period was also noted from the paper record. The total signal strength recorded during each haul was calculated in the following way. For each period of 1000 transmissions the C_2 count was deducted from the C_3 count to give the true C_3 count, and C_1 from C_2 to give the true C_2 count. This was because the C_3 counter counts all signals above the minimum set amplitude, i.e. all the signals which are also counted by C_2 and C_1, while C_2 also counts all the C_1 signals. The true counts for the 3 counters were then raised by their respective microvolt settings, i.e. the minimum recordable signal in each case. The minimum recordable signal rather than the mid points of the range was used for raising, because under the present arrangement the C_1 counter will count from its minimum recordable signal setting up to the theoretical minimum recordable bottom signal, which in this case was 300 microvolts, i.e. 30 db above noise. The total calculated signal for the period was then multiplied by the mean depth squared to compensate for the decrease in signal strength with depth. The resultant values of "signal times depth squared" for each period were summed to give the total for the complete haul.

During these tests the weather was generally fairly rough, so a stalked transducer was used which projects two feet (0·6 m) below the ship's keel,

thus reducing the number of missing signals due to aeration; but 6 hauls were made on 22. July in good weather with the fixed transducer, which CUSHING (in RICHARDSON, *et al.*, 1959) has shown to have a slightly lower noise level than the stalked transducer. Noise of higher amplitude than the general level of about 10 μV occurred from time to time, especially in rough weather, and was mainly associated with the rolling of the ship in a swell. This noise was of a particular type which has been encountered on the R.V. "Ernest Holt", but not on the "Sir Lancelot", and consisted of a series of pulses of high amplitude persisting for the duration of one or two transmissions. This noise was unfortunately recorded by the counters, and it contributed to a fairly high proportion of the counts during hauls in which catches of fish were low; the effect was of less significance during hauls when catches were high. An adjustment was therefore made to each count in the series using the stalked transducer (except for stations 74 and 75 where catches were very high) based on "no fish counts", i.e. periods of 1000 transmissions when no fish signals of countable amplitude were seen on the CRT, and therefore when all counts were due to noise. This identification of fish echoes as distinct from noise was based on two characters: —

1. The slow rise time of a fish signal, which made it look white and rounded, as compared with the sharper and paler noise signal of a quick rise time.
2. The appearance of a fish signal as a recognizable signal, as the target crossed the beam; noise did not appear at the same point twice, nor did it appear in sequences.

The noise counts of these "no fish" periods were deducted from the total noise and fish counts during the other periods of the same haul. No adjustment for noise was made to the counts of the fixed transducer series, because only one "no fish count" was obtained; moreover, catches were relatively high, duration of hauls low, weather conditions reasonable and thus noise low.

The results for the 15 hauls are given in Table 1 and plotted in Figure 5 against the square root of the catch in baskets.

It can be seen in Figure 5 that with the fixed transducer there was a very consistent variation in total signal with catch, except for one station, i.e. No. 67. Notes made at the time record that a very extensive midwater trace was present on the paper record while the trawl was being hauled, and it is possible that fish which had not been counted were caught during this operation. The stalked transducer series shows the same trend as with the fixed transducer, but the points are much more scattered. This is because the adjustment from "no fish counts" is at best only a crude method of compensating for noise, since countable noise could vary quite considerably during any trawl haul in poor weather, depending on the exact heading of the ship in relation to sea and swell.

Discussion

The present counter arrangement worked very well under good weather conditions during fishing operations, but large errors due to noise occurred when the weather deteriorated. This noise was mainly of a particular type encountered on the R.V. "Ernest Holt" and consisted of a series of pulses of high amplitude, persisting for the duration of one or two transmissions when the ship rolled sharply. A solution of the problem could be achieved

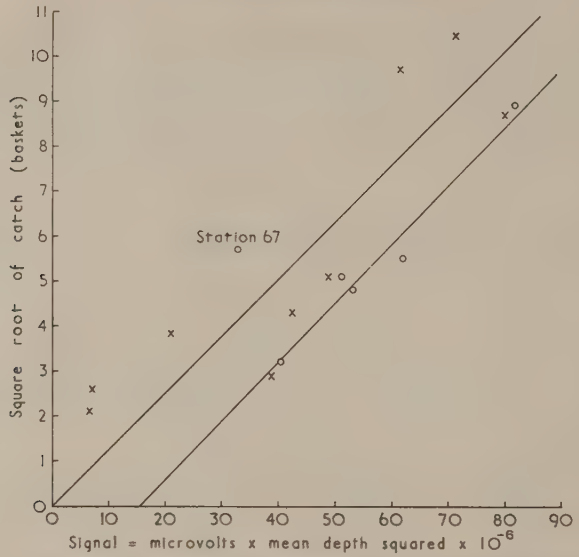

Figure 5. The relationship between catch (square root of baskets) and total signal (microvolts times depth squared $\times 10^{-6}$) as recorded on the West Spitsbergen Banks by R. V. "Ernest Holt", Cruise V, July 1959.
x = stalked transducer.
o = fixed transducer.

Table 1

Echo counts on trawl hauls
R.V. "Ernest Holt", Cruise V, July 1959, West Spitsbergen Banks

Station	Mean depth Fathoms	Mean depth Metres	Duration of haul (minutes)	Catch (baskets) Cod	Catch (baskets) Haddock	Catch (baskets) Total	Square root of baskets	Total signal ($\mu VD^2 10^{-6}$)
A. Fixed transducer								
63	58	106·1	44	9½	½	10	3·2	40·3
64	55	100·6	41	28½	1½	30	5·5	61·8
65	54	98·7	32	78	2	80	8·9	81.8
66	58	106·1	58	25	1	26	5·1	51·0
67	53	96·9	59	31	1	32	5·7	32·5
68	55	100·6	27	22½	1	23½	4·8	53·3
B. Stalked transducer								
54	50	91·4	108	2½	5¾	8¼	2·9	38·4
57	57	104·2	90	73½	1½	75	8·7	79·9
58	52	95·1	92	3¾	¼	4¼	2·1	6·0
59	56	102·4	96	24½	1½	26	5·1	48·8
60	56	102·4	86	14	½	14½	3·8	20·8
61	53	96·9	91	6	1	7	2·6	7·1
70	57	104·2	45	16¼	2	18¼	4·3	42·3
74	54	98·7	56	107½	2½	110	10·5	71·1
75	55	100·6	31	94½	–	94½	9·7	61·4

by having a separate series of "noise" counters, set up in exactly the same way as the fish counters but scanning either the part of the midwater area where no fish were to be found (this could quickly be ascertained from the paper record), or below the bottom clear of any interference from the bottom echo itself or any secondary echo. In this way an accurate noise count could be obtained, which when deducted from the fish and noise count would leave a really accurate count of the actual fish signals.

Nevertheless the automatic fish echo counting system represents a considerable advance from the visual counting method used hitherto (RICHARDSON, *et al.*, 1959), both in the accuracy of the signal data recorded and in operator's time. While this applies particularly to counts made on trawl hauls, there is no reason why the same accuracy should not be obtained on echo surveys, provided that significant changes in the depth of the seabed do not occur over such short periods that the operator cannot keep the counting levels adjusted correctly.

Acknowledgments

The basic system which this fish counter employs was the idea of Mr. R.W. WOODGATE, formerly of Pye Marine Ltd. A prototype was developed by him and supplied by Pye Marine to the Fisheries Laboratory, Lowestoft, in 1957.

Summary

1. An automatic system for counting fish echoes close to the seabed is described. This system eliminates loss of information which was inherent in the visual method of counting used hitherto.

2. Tests made with this system during fishing operations on the West Spitsbergen Banks showed a close relationship between trawl catches and counted fish signals under good weather conditions.

Reference

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The Effect of Pressure on the Survival and Distribution of Larval and Young Fish

By

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Introduction

This work is one of a series of studies carried out on the effect of the different environmental factors on the very early stages of some marine and freshwater fish (Bishai, 1960a–d, 1961). The aim of this study is to find an explanation for the behaviour of the early larval stages of fishes under natural conditions. Such early stages — which are considered as being critical in the life of a fish — may react differently to the various factors as compared with older stages. Little work has been done on the early larval stages and therefore it was found necessary to carry out the present investigation. The results of this experimental study may throw light on our knowledge on the behaviour, distribution, and survival of the early larval stages of fish in their natural environment.

In the present investigation the effect of pressure (either higher or lower than one atmosphere) was studied in order to find out the behaviour and reaction of fish at different ages to compression and decompression. The results of this study are compared with the previous work.

The effect of pressure on the survival and distribution of larval and young fish was studied experimentally by A. Dannevig and G. Dannevig (1950), Dannevig and Hansen (1952), and Henly (1952). They found that cod larvae respond to changes in water pressure as soon as the yolk-sac was absorbed. In addition, cod larvae could not be reared in shallow aquaria as high mortality took place when they were 3–6 weeks old. A similar observation was mentioned by McIntosh and Masterman (1897) who pointed out that cod larvae move into midwater and later to the bottom after the yolk-sac absorption.

The response of fish larvae to pressure seems to depend on the presence or absence of a swimbladder. Thus cod and other physoclistous (closed swimbladder) larvae are affected by pressure in a different way to either herring larvae (physostomous, open swimbladder) or plaice larvae (no swimbladder).

The importance of the study of the swimbladder in the early stages of development was emphasized by SCHACH (1939), A. DANNEVIG and G. DANNEVIG (1950), HENLY (1952), JONES and MARSHALL (1953), and JONES (1957). The latter authors gave a recent review on the swimbladder and its function and showed that the presence or absence of the swimbladder is one of the most important factors affecting fish distribution. Thus while those with a closed swimbladder are restricted in their vertical movements (MOREAU, 1876; JONES, 1951, 1952; SCHOLANDER, *et al.*, 1951; and JONES and MARSHALL, 1953), those with an open swimbladder live mostly near the air water interface where they can swallow air bubbles from the air. Fish without a swimbladder can move freely in the water. JONES and MARSHALL (1953) pointed out that the presence of a swimbladder in the early stages of some fish may be very important in connection with the type of life they are living. CUNNINGHAM (1896) and KYLE (1913) showed that the larvae of flat fishes with well developed larval swimbladder have a fairly long pelagic life as compared with those larvae without a swimbladder. Thus there is a correlation between the development of the swimbladder and the duration of the pelagic phase.

The initial filling of the swimbladder with gas was studied by many investigators (VOGT, 1842; VON LEDEBUR, 1928; WUNDER, 1935; VON LEDEBUR and WUNDER, 1937; JACOBS, 1938, etc.), who found that the swimbladder is first filled with air bubbles swallowed by the fish and passing through the pneumatic duct. JACOBS (1938) believed that the swallowed air does not entirely fill the swimbladder but it stimulates the production of gas by the gas gland. MCEWEN (1940), however, thought that the first filling of the swimbladder can take place even if some physoclists were not given the chance to reach the surface. JONES and MARSHALL (1953) emphasized the importance of the study of the way in which the swimbladder is first filled with gas, and its correlation with the development of the pneumatic duct and the ecology of the larvae. Since the gas regulation in the swimbladder is under nervous control (MOREAU, 1865, 1876; BOHR, 1894; KUIPER, 1915; JACOBS, 1932; FRANZ, 1937; and FÄNGE, 1953), the extent of development of such nerves in the early larval stages is relevant to their behaviour.

The effect of pressure on physostomes differs from that on physoclists, because in the former adjustment to pressure change can be made by swallowing or releasing gas bubbles through the pneumatic duct (MOREAU, 1876; GUYÉNOT, 1909; KUIPER, 1915; EVANS and DAMANT, 1929; JACOBS, 1934; FRANZ, 1937; and JONES and MARSHALL, 1953). Salmonidae are among the physostomes (VOGT, 1842; HOAR, 1937; and JONES and MARSHALL, 1953) which have a poorly developed retia mirabilia (CORNING, 1888; DE BEAFORT, 1909; RAUTHER, 1922; MAIER and SCHEURING, 1923; and JONES and MARSHALL, 1953). JACOBS (1938) noticed that salmonids were unable to replace gas lost from the bladder when prevented from reaching the surface.

The effect of *decompression* (pressure reduction) on fish may cause them to develop well marked symptoms which are often termed "gas disease" or "decompression sickness". These symptoms comprise the formation of gas bubbles in the heart and blood vessels, under the skin and over the fins, and the eyes bulge due to the accumulation of gas behind them. This gas disease is not only caused by changes in pressure (HOPPE-SEYLER, 1857; GORHAM, 1899 a & b; MARSH and GORHAM, 1905; DAMANT, 1920; VON LEDEBUR, 1936; WALLS, 1942; JONES and MARSHALL, 1953; and DOUDOROFF, 1957), but is also

due to supersaturation of water with gas (Osgood, 1904; Marsh and Gorham, 1905; Shelford and Allee, 1913; Semper (in Henly, 1952); Plehn, 1922; Roth, 1922; Mřsic, 1933; Haempel, 1937; A. Dannevig and G. Dannevig, 1950; Dannevig and Hansen, 1952; Henly, 1952; and Doudoroff, 1957).

Many authors have observed that the occurrence of gas disease was related to the presence of swimbladder (Gorham, 1899a; Marsh and Gorham, 1905; Damant, 1920; von Ledebur, 1936; and Jones and Marshall, 1953). The latter authors stated that "only fish with swimbladder are affected by decompression and the degree to which the symptoms develop varies from species to species and with the depth from which they were taken".

Many explanations were put forward to explain how decompression causes gas disease: —

1. Due to temperature change within the body, i.e. the venous circulation being warmer (Marsh and Gorham, 1905). These authors pointed out that when a fish with swimbladder is brought up to the surface, it may not be able to get rid of the gas quickly through the gills and gas bubbles may be released in the blood due to temperature differences within the body.

2. Disengagement of gas from the tissues of the fish during decompression (Verrier, 1931; Rabaud and Verrier, 1931, 1932b & c, 1933a & b, 1934a–d; and Doudoroff, 1957).

3. Jones and Marshall (1953) did not agree with Rabaud and Verrier's views. They suggested the following two explanations for the development of the symptoms of the gas disease but were not able to say which of the two was the more likely to be correct.

(a) Blood and tissues can be saturated with gas by resorption of the gas through the oval; once saturated any further reduction of pressure would lead to the formation of gas bubbles (in the body cavity, beneath the skin or behind the eyes, etc.).

(b) A reduction in pressure might rupture the swimbladder wall (Jones, 1949) and bubbles of gas might, therefore, enter into the broken blood vessels giving rise to symptoms of decompression sickness throughout the body of the fish.

Apparatus and Technique

Previous methods were mainly concerned either with the study of the behaviour of fish under pressure or on the effect of decompression. Plattner (1941) studied the effect of decompression by using a flask filled with water placed in a chamber in which the pressure could be reduced. Dijkgraaf (1942) in his study on the effect of pressure used a maximum pressure of 50 cm Hg. Jones (1952) used an apparatus in which a continuous water flow was maintained and the fish were subjected to a total pressure of 131 cm Hg. Reduction of pressure in this apparatus was achieved by releasing a flow control clip. For decompression Jones (1952) used a vacuum pump connected to his experimental tank.

In the present investigation two apparatus were used: one for pressure in which the fish can be subjected to a total pressure of 170 cm Hg (i.e., atmospheric pressure plus 94 cm Hg); the other apparatus is for decompression in which fish can be subjected to a pressure of 10 cm Hg.

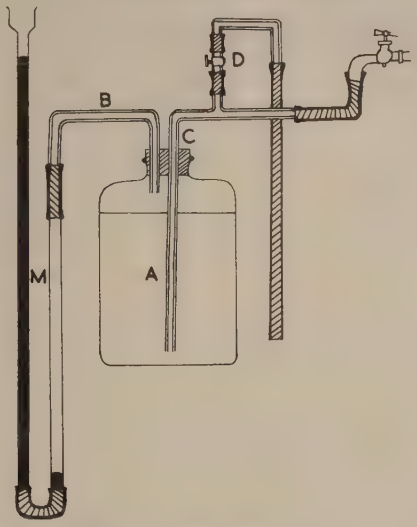

Figure 1. Apparatus for subjecting larval and young fish to a total pressure of 170 cm Hg.

1. Apparatus for compression

In this apparatus the pressure of the tap water was used which once achieved in the experimental tank would remain when the tap was closed. However, there was no water circulation. In this apparatus air was left over the water so as to allow the fish to gulp air at the surface thus entering into hydrostatic equilibrium much more quickly than if they had to secrete the gas themselves. The difficulty in using this method is that the experimental water as well as the blood and tissues of the fish will be supersaturated with gas.

The apparatus consisted of a thick-walled glass experimental vessel of 6 litres capacity closed by a two-hole rubber bung. Through one of the holes passed a capillary tube B of 8 mm thickness and 2 mm inner diameter (see Fig. 1). The tube was attached to a mercury manometer M. In the other hole a tube C was placed which was also a capillary tube of the same dimensions as B. Tube C was T-shaped with one limb bent down so as to reach the bottom of the experimental vessel, and the other limb connected to the tap by rubber pressure tubing. To the third limb a stop-cock D was fixed controlling the outflow to waste. All connections consisted of pressure tubing.

For pressure higher than two atmospheres Dr. H. O. BULL's pressure tank (unpublished work) was used where fish can be subjected to pressure as high as 8 atmospheres.

2. Apparatus for decompression

This consisted of the same experimental vessel A of 6 litres capacity closed by a two-hole rubber bung through which passed a tube B connected to the

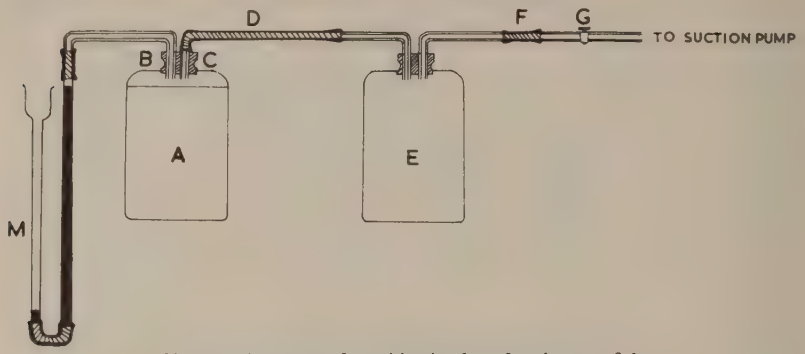

Figure 2. Apparatus for subjecting larval and young fish to pressures below one atmosphere.

mercury manometer M and a tube C connected by the pressure tube D to a 6 litre reservoir E for pressure regulation. The latter was connected to a suction pump through pressure tubing F provided with a stop-cock G (see Fig. 2).

In neither apparatus was there any water renewal. This was found unnecessary as fishes used in the experiment (either early larval or post-larval stages or even young fish) could live in this apparatus for a period from a week to a fortnight (in some cases for 25 days) without any apparent ill-effects. In every case control experiments were carried out.

Procedure

1. Compression

The fish larvae or young fish were placed in the experimental bottle two-thirds full of well aerated water (fresh or sea water). The rubber bung was then fitted tightly into the neck of the bottle, made possible by pushing the glass tube B into position only after fitting the rubber bung. After connecting with the tap, stop-cock D was closed and the fish were left in the experimental bottle for two hours before starting the experiment. The tap was then opened slightly to cause a slow increase of pressure. The period of augmenting the pressure to the desired level was regulated by manipulating the tap. After the required pressure had been reached (measured by the mercury manometer) the tap was closed. The volume of water in the experimental bottle increased owing to the water introduced from the tap. But about a litre of air was left over the surface of water. The reactions of the fish associated with the increase of pressure could now be recorded. When using pressures of 160 cm Hg there was occasionally a slight loss of pressure (i.e., 1–2 cm Hg) but this was easily corrected. In experiments with marine fish larvae and young fish, some tap water entered the experimental vessel causing a decrease in salinity. It was found, using a pressure of 160 cm Hg, that the salinity changed from 33‰ to 29‰ which, however, was not harmful to the experimental fish as shown by experiments on the same fish using low salinities (BISHAI, 1961).

At the end of the experiment the pressure was released by opening stop-cock D, slowly or quickly according to the requirements of the observations on the reaction of the fish to decreasing pressures.

2. Decompression

After introduction of the fish into vessel A, the apparatus was prepared for the experiment by connecting it to the manometer, and to the suction pump and opening stop-cock G. Once the desired pressure level was reached stop-cock G was closed. To restore the former pressure stop-cock G was partly opened.

In all experiments the oxygen tension, hydrogen ion concentration, and salinity (in case of marine fish) remained within the limits of toleration of the fish. The only change was that of the pressure. In experiments on young fish, which lasted for long periods, food in the form of living animals was introduced into the experimental vessel. In all experiments the pressure is either given in atmospheres or cm Hg. The pressure under which the fish is subjected is the total pressure, i.e. 2 atmospheres means the atmospheric pressure plus 1 atmosphere increase in pressure.

Table 1

Species	Temperature °C	Length of larvae (mm)	Age (days)
Clupea harengus L.	13·1–14·8	6·5– 8	1– 9
Salmo salar L.	7·9–12·5	20 –25	1–42*)
Salmo trutta L.	5 –10·5	18 –24	1–42*)
Salmo trutta f. *fario*	5 – 9·2	16 –25	1–42*)

*) Yolk-sac absorbed 28–35 days after hatching.

Material

The fish larvae and young used in these experiments were herring (*Clupea harengus* L.); salmon (*Salmo salar* L.); sea trout (*Salmo trutta* L.), and brown trout (*Salmo trutta* f. *fario* L.). These fish were reared at the Dove Marine Laboratory, Cullercoats, England. The artificial fertilization was carried out at sea or at fish hatcheries. Methods of rearing these fish larvae are given in a separate paper (Bishai, in press). Young plaice (*Pleuronectes platessa* L.) ranging from 37–50 mm collected from near the Laboratory were also used.

The average lengths of the larvae used and the temperatures at which they were reared were as shown in Table 1.

Rearing of the salmonids was continued at an average temperature of $13{\cdot}2° \pm 2{\cdot}5°C$.

Experimental Results

I. Compression Experiments

A. Herring Larvae

1. Pressure from 1–2 atmospheres

Two experiments were carried out in the pressure apparatus using 50 newly hatched larvae together with their food (*Artemia salina* larvae and *Tigriopus fulvus*). Each experiment lasted for 12 days at an average temperature of 14·8°C. The pressure was raised from 1 atmosphere (75·7 cm Hg) to 2 atmospheres (151·5 cm Hg) in ten minutes. During compression the larvae behaved normally swimming most of the time near the surface. Mortality began on the 7th day but was the same as in the control experiments. However, larvae under pressure, although not feeding, lived longer than those under normal conditions. On the 12th day the pressure was released in ten minutes. During decompression the larvae behaved normally and continued to live for a few days. Gas bubbles were not released from the larvae. At this stage (newly hatched to 12 day-old) the swimbladder is not yet developed. Examination of the blood capillaries of the larvae after decompression was not carried out as the larvae continued to live normally as in the controls.

2. Pressure from 2–4 atmospheres

This experiment was carried out in Bull's pressure tank using two finger bowls each containing 12 newly hatched larvae. A third bowl containing larvae was left at room temperature as a control. On the first day the pressure was raised in 10 minutes to 2 atmospheres; 3 atmospheres on the second, 4 atmospheres on the third day. The experiment lasted for five days at an average temperature of 15·5°C. The larvae were behaving normally both during compression or when under pressure. On the 5th day the pressure, which had been dropping gradually since the 4th day, was released in 30 minutes. The larvae behaved normally and did not seem to be affected by decompression. Analysis of the water showed a high content of oxygen (120% saturation at NTP and a little change in the pH (from 8·00 to 7·85)). No gas disease was observed due to pressure reduction. In addition the formation of air bubbles in the supersaturated water did not take place.

B. Young Plaice

(3·7–5·0 cm long)

Seven experiments were carried out using two or three fish in each case, together with their food (*Artemia salina* larvae and *Tigriopus fulvus*). The experiments lasted for 2 days (2 experiments); 3 days (1 experiment); 6 days (1 experiment); and 8 days (3 experiments). All experiments were performed at 16·5 to 18·3°C and at a pressure of two atmospheres (from 154·2 to 159·5 cm Hg, i.e. atmospheric pressure plus 76·5 cm Hg). The rise of pressure took place quickly (from 5 to 10 minutes). During compression as well as during the experiment the fish lived normally without showing any ill-effects.

At the end of each experiment, although decompression took place quickly, (from 5 to 10 minutes), the fish did not seem to be affected. They behaved normally, passing most of the time near the bottom, but sometimes showing

an increase in their respiratory movements. No gas bubbles were seen either inside or outside the body of the fish and no gas bubbles were released. The oxygen content of the water at the end of the experiment ranged from 82 to 70% oxygen saturation. After decompression the fish continued to live normally without any mortality.

C. Salmon, Sea Trout, and Brown Trout

1. Pressure from 1–2 atmospheres

(i) Newly hatched larvae

(a) Ten newly hatched sea-trout larvae were subjected to a gradual rise in pressure from 1 to 2 atmospheres. The rise in pressure took 9 days after which the experiment was continued for three days at an average temperature of 16·1°C. During the experiment the larvae behaved normally without showing any sign of discomfort. On release of the pressure on the 12th day, the larvae became very active for a while, swimming vigorously upwards. They did not, however, show any ill-effects and lived normally without developing any gas disease.

(b) Five newly hatched larvae of each species were subjected to quick rise of pressure. The pressure was raised from 1 to 2 atmospheres (154 cm Hg) in twenty minutes. With increase of pressure the larvae showed unusual activity by swimming vigorously near the bottom. Such activity continued for one hour, after which the larvae were again behaving normally.

The experiment lasted for 25 days at the end of which the pressure was reduced to one atmosphere in 10 minutes. During decompression the larvae did not show any discomfort and they lived normally without showing any disease. One brown trout was seen swimming near the surface during decompression and continued to do so for the first 24 hours after the end of decompression. Then it spent most of its time near the bottom. The swimbladder, which developed in these larvae, can be easily seen through the body wall.

In these experiments food was not given to the larvae as they do not feed at this stage and the yolk-sac was absorbed 28–35 days after hatching.

(ii) 30 day-old larvae (yolk-sac nearly absorbed)

Five larvae of each species, together with their food (live *Daphnia*) were subjected to a quick rise of pressure. The pressure was raised from 1 to 2 atmospheres in 30 minutes. During the experiment, which lasted for 18 days at an average temperature of 13°C, all the fish behaved normally. On reduction of pressure (i.e., from 2 to 1 atmosphere) which took place in 20 minutes, all the fish showed increased activity but none died. Some of the larvae, especially those with the completely absorbed yolk-sac, were seen swimming near the surface after the end of decompression. Although the swimbladder is well developed at this stage, the release of gas bubbles was not observed. In addition gas bubbles were not formed on the walls of the experimental tank after decompression.

(iii) 56 day-old larvae

Five larvae of each species, together with live *Daphnia* were introduced into the pressure apparatus in which the pressure was raised to 2 atmospheres in

15 minutes. The experiment lasted for 8 days at an average temperature of 16·1°C. On the 8th day reduction of pressure took place in two hours. As soon as decompression started most of the fish were swimming or even floating on the surface. Gas bubbles began to appear on the walls of the experimental vessel. Ten minutes after the end of pressure reduction, two salmon and two sea trout showed distress by bending their bodies quickly and then floated on the surface. Examination of these fish showed the presence of air bubbles inside the mouth, behind the gills, and within the viscera. The rest of the fish had their swimbladder distended and some had gas bubbles attached to their bodies. In no case was the release of gas bubbles from the mouth of the fish observed. All fish were placed in a jar through which air was bubbled overnight. In the morning (after 16 hours) all the larvae were alive and healthy, their swimbladders were normal and no gas disease developed among them.

(iv) 98 day-old brown trout

Two experiments were carried out in which two fish were subjected to a quick rise of pressure (i.e., from 1 to 2 atmospheres in 5 minutes). At the beginning of compression the fish remained motionless at the bottom. The fish never swam near the surface. After half an hour the respiratory movements increased. The fish showed discomfort, occasionally gulping, and bended their bodies. After 6 hours of compression the fish were showing regular but sudden gulping movements. Then they died 16–22 hours after compression. Analysis of the experimental water before and after the experiment showed no significant change either in the oxygen content or pH value. The swimbladder at this stage is well developed.

Two control experiments were carried out; one using the same volume of water but in another jar, and the other using the same water in which the fish died. In both experiments the fish lived for a week without being fed.

(v) 102 day-old brown trout

A fish was subjected to a slow rise of pressure, i.e. from 75·5 cm to 103·5 cm Hg (+ 28 cm Hg or 0·36 atmosphere) in 5 hours. After 17 hours at the highest pressure the fish died.

(vi) 105 day-old brown trout

Two fish were subjected to a gradual increase of pressure, i.e. from 75·9 cm to 116·4 cm Hg (+ 40·5 cm Hg or 0·53 atmosphere in 30 minutes). Two hours after raising the pressure the fish died.

(vii) 133 day-old brown trout

Three experiments were carried out subjecting the fish to a quick rise of pressure, 37 cm Hg (0·48 atmosphere in 5 minutes) and 15 cm Hg (0·19 atmosphere, 2 experiments). In the first experiment the fish died after 13 hours. In the 2nd and 3rd experiments (i.e., 15 cm Hg increase of pressure) the fish, although living for 17 hours, were more or less moribund, staying at the bottom and laying on its side. On releasing the pressure air bubbles were seen coming out from the mouth of the fish, but they were still alive.

(viii) 178 day-old salmon

Two experiments were carried out, as in No. vii, placing a salmon with the brown trout and subjecting them to 37 and 15 cm Hg increase in pressure. While the salmon lived in the first experiment for 12 hours (duration of experiment) it died in the second after 5 hours of restoring the new pressure (i.e., 1 atmosphere plus 15 cm Hg).

(ix) 272 day-old brown trout

Two fish together with their food (live *Daphnia*) were subjected to a quick increase in pressure, i.e. from 1 to 2 atmospheres in 10 minutes. During compression the fish were very active, occasionally visiting the water surface and gulping air. After going up to the surface, the fish usually went to the bottom where they showed rapid spasmodic respiratory movements. 15 minutes after reaching the experimental pressure of 2 atmospheres the fish rested at the bottom where they remained quiet. The experiment lasted for 7 days at an average temperature of 16·5°C. At the end of the 7th day reduction of pressure was carried out slowly taking 80 minutes (i.e., from 157 cm Hg to 74·4 cm Hg). During decompression emission of small gas bubbles either from the mouth or from behind the gill covers was observed (11 bubbles from the mouth and 5 from behind the gill covers). The fish, which were resting at the bottom, no longer took up a horizontal position. The body was inclined to the bottom with the tail well above the head. The fish were trying to keep themselves at the bottom by pushing their nose at the bottom, but they poised a few centimetres off the bottom. After 33 minutes of the beginning of decompression (atmospheric pressure plus 30 cm Hg) the fish appeared to be disturbed and excited, swam upwards and made occasional visits to the bottom. Sixteen minutes after the end of decompression the fish were floating at the surface upside down. Then their respiratory movements stopped suddenly and they died. Their bodies were intact and no gas bubbles were seen inside the fins, blood vessels or heart. However, tiny bubbles of gas appeared on the body of the fish. These bubbles which were formed due to separation of gas from the water caused by decompression, were seen attached to any particle inside the experimental bottle.

(x) 220 day-old salmon

A fish together with its food (live *Daphnia*) were placed in water in which oxygen was bubbled for 15 minutes. The aim of this experiment was to find out the effect of water supersaturated with oxygen (after compression) on young fish. Compression from 1 to 2 atmospheres took place in 35 minutes during which the fish was very active, swimming frequently near the surface. The fish was seen swallowing air bubbles by pushing its head above the surface of water. The fish which was very active and excited for 15 minutes — after the end of compression — went to the bottom and remained quietly till the end of the experiment which lasted for 7 days at an average temperature of 14·85°C.

On the 7th day decompression was carried out slowly taking 145 minutes (from 2 to 1 atmospheres). During decompression the escape of gas bubbles from mainly behind the gill covers was observed (15 bubbles from behind the

gill cover and 1 from the mouth). The fish, which was resting most of the time near the bottom, showed quick respiratory movements. After 120 minutes from the beginning of decompression the fish which was disturbed and restless began to swim near the surface. Then it went to the bottom. At the end of decompression (i.e., atmospheric pressure) the fish was still alive, but 15 minutes later it swam suddenly, jumped and showed signs of distress. The fish then floated on the surface upside down and died. The dead salmon sank to the bottom at an increase of pressure of 11·5 cm Hg (i.e., 1 atmosphere plus 11·5 cm Hg). Gas bubbles began to accumulate on the body of the dead fish. Examination of the fish showed the presence of a large gas bubble inside the mouth, and two elongated gas bubbles inside the caudal fin. No gas bubbles were seen either inside the gills, the skin, or viscera.

2. Pressure from 3–5 atmospheres

(i) 17 day-old larvae

Ten larvae of each species (salmon, sea trout, and brown trout) were introduced into the pressure tank. The larvae were placed in rectangular dishes 10″ long, 6″ wide, and 2″ high. The experiment lasted for 12 days at an average temperature of 15·2°C during which the fish were subjected to the following pressures: —

Duration of pressure (days)	Total pressure to which larvae were subjected (atmospheres)
1	3
3	4
1	3
3	4
2	5
1	4
1	3

The increase in pressure took one hour for every atmosphere. During compression and throughout the experiment the fish behaved normally without showing any sign of discomfort. On the 13th day, reduction of pressure took place from 3 to 1 atmospheres in 30 minutes. All larvae showed signs of discomfort by increased activity. However, none of the larvae died either due to compression up to 5 atmospheres, or due to decompression. Neither was the release of gas bubbles from the larvae observed. Towards the end of the experiment the swimbladder was well developed. During the experiment food was not given to the larvae as the yolk-sac was not completely absorbed and the larvae did not take food during this stage. After decompression all the larvae continued to live normally.

(ii) 195–220 day-old salmon and brown trout

Two fish, one of each species, were placed in the pressure tank together with their food (live *Daphnia*). Compression took place gradually, i.e. it took 3 days to raise the pressure from 1 to 4 atmospheres. The increase in pressure for every atmosphere took one hour. The pressure under which the fish were subjected was as follows: —

Duration of pressure (days)	Total pressure to which fish were subjected (atmospheres)
1	2
1	3
2	4
1	3
1	2
1	1

The fish which were behaving normally before any rise of pressure, became excited and active when compression began and were seen coming to the surface of water apparently gulping air. After the 3rd day the salmon was eaten alive by the trout. On the 4th day decompression was allowed to set in slowly and it took 24 hours for each atmosphere reduction. On the 7th day the young trout floated on the surface upside down with the ventral wall ruptured and the stomach bulging out. Examination of the fish showed the presence of gas inside the stomach. The swimbladder, although distended with gas, did not rupture. No gas bubbles were seen inside the fins or blood vessels.

II. Decompression Experiment

Pressure below one atmosphere

In addition to those experiments in which the fish were subjected to pressure reductions down to one atmosphere, one experiment was carried out to find out the effect of pressures below one atmosphere. For this experiment a 103 day-old brown trout was used. The young fish was placed in the decompression apparatus and the pressure was reduced slowly, i.e. from 75·8 cm Hg to 25·8 cm Hg in 260 minutes. During decompression gas bubbles were released either from the mouth or from behind the gill covers. 180 minutes after the beginning of decompression, gas bubbles began to appear on the body of the fish. To get rid of these bubbles the fish swam in the water. The formation of gas bubbles was also seen on the walls of the experimental vessel as well as on any particle present in the water. Although the fish made occasional visits to the surface it mainly remained at the bottom.

At the end of decompression the normal pressure was restored (i.e., atmospheric pressure) during which the fish seemed restless and swam near the surface. The next morning (after 16 hours) it had recovered.

A summary of the experimental results is given in Table 2.

Discussion

My results show that newly hatched herring larvae (6·5–8 mm long) and salmonid alevins (until the yolk-sac is nearly absorbed) can live at pressures as high as 5 atmospheres (corresponding to a depth of 40 m) and that they are apparently not affected by compression either quick or slow. However, young salmon and brown trout (98–178 day-old) die within 24 hours when subjected to an increase of pressure of more than 15 cm Hg (0·19 atmosphere). This is difficult to explain as at this stage the young fish have a well developed open swimbladder. Moreover, if they are subjected to an increase of pressure

Table 2

The effect of pressure on larval and young fish
Summary of the experiments described in the text

Experiment	Species	Age or size	Swimbladder	Experimental treatment (Pressure in atmospheres)	Results	
					Compression	Decompression
A-1	Herring	Newly hatched (6·5–8 mm)	Not developed	+ 2	Lived	Lived
A-2	Herring	Newly hatched (6·5–8 mm)	Not developed	+ 4	Lived	Lived
B	Plaice	37–50 mm	Absent	+ 2	Lived	Lived
C-1 (i)	Salmon, sea trout, and brown trout	Newly hatched (16·20 mm)	Not well developed	+ 2	Lived	Lived
C-1 (ii)	Salmon, sea trout, and brown trout	30 day-old	Well developed	+ 2	Lived	Lived
C-1 (iii)	Salmon, sea trout, and brown trout	56 day-old	Well developed	+ 2	Lived	Lived
C-1 (iv)	Brown trout	98 day-old	Well developed	+ 2	Died	—
C-1 (v)	Brown trout	102 day-old	Well developed	+ 0·36	Died	—
C-1 (vi)	Brown trout	105 day-old	Well developed	+ 0·53	Died	—
C-1 (vii)	Brown trout	133 day-old	Well developed	+ 0·48	Died	—
C-1 (vii)	Brown trout	133 day-old	Well developed	+ 0·19	Lived for 17 hours	Lived
C-1 (viii)	Salmon	178 day-old	Well developed	+ 0·19	Died	—
C-1 (viii)	Salmon	178 day-old	Well developed	+ 0·48	Lived for 12 hours	Lived
C-1 (ix)	Brown trout	272 day-old	Well developed	+ 2	Lived	Died
C-1 (x)	Salmon	220 day-old	Well developed	+ 2	Lived	Died
C-2 (i)	Salmon, sea trout, and brown trout	17 day-old	Not well developed	+ 5	Lived	Lived
C-2 (ii)	Salmon	195 day-old	Well developed	+ 4	Lived	—
C-2 (ii)	Brown trout	220 day-old	Well developed	+ 4	Lived	Died
Section II	Brown trout	103 day-old	Well developed	− 0·66	—	Lived

following decompression to less than one atmosphere (i.e., from 25·7 to 75·7 cm Hg) they seem to be less affected. Several experiments were carried out (experiments Nos. C-1 (iv) to C-1 (viii)) at this stage — subjecting the fish to an increase of pressure of more than one atmosphere — and in all cases the fish died. The death of the young fish could not be due to supersaturation of the experimental water as analysis showed no significant change in its oxygen content or the

pH. Later stages of salmonids (older than 178 days) are not affected under the same conditions by the increase of pressure. It is concluded that the reaction of young salmonids towards the increase of pressure depends on the age of the fish. Thus, while the alevins are not affected until the absorption of the yolk-sac, young fish from 98–178 days old are affected, while older stages are not affected.

Young plaice (3·7–5 cm long) tolerate pressures at least as high as two atmospheres (higher pressures were not investigated). Plaice do not have a swimbladder and thus they are not affected by the increase of pressure. It is concluded that the distribution of plaice at this stage is not affected by pressure.

It is clear that the effect of decompression on fish differs according to the species and age. In addition, the presence or absence of a swimbladder seems important. In the present investigation newly hatched herring larvae, salmonid alevins as well as young plaice were studied. In newly hatched herring larvae the swimbladder is absent and not yet developed. FULTON (1906) pointed out that there is no trace of the swimbladder in newly hatched herring larvae. Later MAIER and SCHEURING (1923) found that the swimbladder bud first appears in herring larvae at 9–10 mm stage. In salmonids, the swimbladder is not well developed in the early larval stages (3 weeks after hatching), but it is well developed in older stages (4 weeks after hatching). The swimbladder of salmonids is of the open type.

The results showed that newly hatched herring larvae (6·5–8 mm long) are not affected by decompression, either quick or slow, although they were subjected to a reduction of pressure of 3 atmospheres. After decompression the larvae continued to live normally. Thus pressure is unlikely to affect the distribution of newly hatched herring larvae and goes to confirm field observations which show that herring larvae undertake a diurnal vertical migration (JOHANSEN, 1925, 1927; and BURD and LEE, 1951). During decompression gas bubbles were not seen on the larvae or inside them. Neither was there a release of gas bubbles from the larvae.

Until the pre-feeding stage, salmonid alevins are not affected by quick or slow decompression. Although the alevins were subjected to a pressure reduction of 3 atmospheres, they continued to live normally after decompression. In some cases gas bubbles were seen attached to the fish but these bubbles came from the water which was supersaturated with gas. Such gas bubbles attach themselves to the walls as well as any solid object inside the experimental tank. One fish that died a day before decompression, was seen to be covered all over with tiny gas bubbles when decompression took place, which caused it to float. The bubbles covering the body of the dead fish could not be due to diffusion of gas from inside the tissues as RABAUD and VERRIER (1932b & c, 1933a & b, and 1934a–d) claimed. My observations confirm the earlier findings of many authors (MEIERHANS, 1935a–c; GUYÉNOT and PLATTNER, 1938, 1939; PLATTNER, 1937, 1938a & b, 1941; and JONES and MARSHALL, 1953).

Salmonid fry are affected by decompression in a different way than that shown by the younger stages. In experiment No. C-1 (iii) where 56 day-old alevins were used, the gas bubbles which were seen inside the mouth and behind the gill covers were separated from the water, due to decompression, and were swallowed by the fish which could not get rid of them. The fish died from asphyxia. It was also noticed that all fish had distended swimbladders and at no time the release of gas bubbles from the mouth or from behind the gill

covers was observed. This suggests that the sphincter mechanism which controls the release of gas bubbles from the pneumatic duct was not fully developed at this stage. The fish with distended swimbladders recovered when left for 16 hours. Such experimental conditions are not met by the fish in nature as the alevins live in shallow water streams and come only to the surface for filling their swimbladders.

Older stages of brown trout (i.e., 103 day-old) do not seem to be affected by pressure reductions of less than one atmosphere. Gas bubbles are released from the mouth and from behind the gill covers. However at older stages (i.e., 220–272 day-old, experiments Nos. C-1 (ix) and C-1 (x)) the young fish are affected by pressure reduction of more than one atmosphere. Fish living at a pressure of two atmospheres usually die either immediately or soon after decompression when the pressure is reduced to one atmosphere (i.e., atmospheric pressure). The fish show signs of distress by jumping and gulping, after which they float upside down. Although the fish have an open swimbladder they die after quick or slow decompression. This may be attributed to the speed of decompression mechanically blocking the sphincter. Thus all the gas cannot escape from the swimbladder and the fish floats helpless on the surface of water. On decompression the release of gas bubbles from the mouth or from behind the gill covers was noticed. However, the gas escaped from the bladder was not sufficient to keep the fish in hydrostatic equilibrium under the new pressure. Gas was also noticed inside the gut. This gas was swallowed by the fish during compression. Similar observation was recorded by Frisch and Stetter (1932) and Guyénot and Plattner (1938) who found that air was retained in the intestine of the fish.

The formation of gas bubbles inside the caudal fin of young salmon (experiment No. C-1 (x)) after decompression may be attributed to: (a) The rupture of the swimbladder causing the entrance of gas bubbles into the broken blood vessels (Jones, 1949 and Jones and Marshall, 1953). This is not the case in the present investigation as the swimbladder was found intact. (b) Gas coming out of the fishes' blood and tissues. Under experimental conditions both water and blood and tissues of the fish become supersaturated with gas. On decompression gas bubbles not only separate from the water but also inside the tissues and blood capillaries of the fish. Thus the death of the fish is due to the decompression sickness. Nitrogen may not be the only gas which causes the gas disease as Marsh and Gorham (1905) claimed, as carbon dioxide is an important factor in the initiation of the formation of gas bubbles in the early stages which are later maintained by nitrogen (Harris, *et al.*, 1945). However, bubbling oxygen in the experimental water, to expel the oxygen, (experiment No. C-1 (x)) did not diminish the development of the gas disease. Harris, *et al.* (1945) found that the use of pre-oxygenated water before decompression reduces the incidence of bubble formation in decompressed bullfrogs.

Young plaice (3·7–5 cm long) were not affected by decompression. Contrary to Rabaud and Verrier (1932b and 1934d) finding, although young plaice were subjected to quick decompression, gas bubbles were neither observed to escape from the mouth nor to cover the body. The fish continued to live normally after decompression, which indicated that bubbles were not formed in the blood capillaries although the water in which the fish were living was supersaturated with gas. Dannevig and Hansen (1952) found that fine gas bubbles which accumulated in the veins of young plaice (some cm long) were

fatal to them. My observations support the work of former investigators (MEIERHANS, 1935a–c; GUYÉNOT and PLATTNER, 1938; PLATTNER, 1941; and JONES and MARSHALL, 1953) who showed that gas bubbles covering the body of the fish were no more than the extraction of the gas dissolved in the water. JONES and MARSHALL (1953) gave a critical discussion of RABAUD and VERRIER's work.

The formation of gas bubbles inside the tissues of young salmonids, due to decompression, and not in newly hatched herring larvae, young plaice, and salmonid alevins can be attributed to the presence of a swimbladder. While the swimbladder is absent in both newly hatched herring larvae and plaice, it is not completely developed in salmonid alevins, but is well developed in young salmonids. Another explanation that I put forward to account for the non-formation of gas bubbles inside the body of newly hatched herring larvae and salmonid alevins is that the gas can diffuse easily from the blood to the surrounding water through the skin covering the body. Moreover, a relatively larger area is exposed to the water, while young fish are covered with a thick skin so the diffusion of gas outside the body must be impossible or is very much slower. HARRIS, *et al.* (1945) pointed out that large frogs suffer from decompression while small ones do not. This they explained as due to the quicker rate of diffusion of carbon dioxide — which initiates the bubble formation — through the muscles of the small frogs.

It is concluded that the effect of pressure on the survival and distribution of larval and young fish depends on the species, the age of the fish, and the presence or absence of a swimbladder.

Acknowledgements

This work was carried out at the Dove Marine Laboratory, Cullercoats, King's College, Durham University, England. I would like to express my deep gratitude to Dr. H. O. BULL, Deputy Director, for his valuable help and advice, and for allowing me to use his pressure tank without which experiments with high pressures were impossible. Thanks are also due to Mr. A. C. BURD, Fisheries Laboratory, Lowestoft; the Northumberland and Tyneside River Board; Mr. G. L. TATHAM of Welham Park Fish Hatchery, Melton, Yorkshire; Skipper J. JACK and Skipper R. G. DOUGAL for supplying material and the facilities they offered me.

Summary

1. A review of the effect of pressure on larval and young fish is given. Apparatus and methods are described to study the effects of pressure changes on young fish.

2. Newly hatched herring larvae (*Clupea harengus* L.) could live at a pressure of 4 atmospheres. They are neither affected by compression nor by decompression. Thus newly hatched herring larvae can move from deep to shallow water without any ill-effects due to pressure changes even if the water in which they live is supersaturated with gas.

3. Young plaice (*Pleuronectes platessa* L.) are not affected by compression or decompression of at least 2 atmospheres. On decompression the release of gas bubbles was neither observed from the mouth nor from behind the gill

covers, nor did gas bubbles form on the body of the fish although the water in which they were living was supersaturated.

4. The effect of pressure and decompression on salmonids (*Salmo salar* L., *Salmo trutta* L., and *Salmo trutta* f. *fario*) depends on the age of the fish. Until the absorption of the yolk-sac alevins can live under pressures as high as 5 atmospheres. They are neither affected by compression nor by decompression. The release of gas bubbles from the mouth or the appearance of gas bubbles on the body was not observed during decompression although the water in which the fish were living was supersaturated. The swimbladder at this stage is not completely developed.

At an age of 56 days, while the fish can stand pressures of two atmospheres (or perhaps more), they are affected by decompression even at a slow rate. Although the swimbladder is well developed, the release of gas bubbles did not take place on decompression and the swimbladder became distended with gas. This was attributed to the incomplete development of the sphincter mechanism which controls the release of gas bubbles from the pneumatic duct.

Salmon and brown trout 98–178 days old die within 24 hours when subjected to any increase of pressure of more than 15 cm Hg. Older fish (272 days), can live under such pressure as well as at higher pressures (4 atmospheres).

5. The death of young salmonids due to decompression is attributed to the supersaturation of the experimental water with gas. On decompression gas bubbles are separated from the water and attach themselves to the fish. In addition the fish may swallow gas bubbles which block their mouths and the fish die from asphyxia. Death of fish may be due to decompression sickness where gas bubbles are separated from the blood and tissues of the young fish on decompression. The ability of the blood to be supersaturated with gas under pressure may be a character of young fish with swimbladder.

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Otolith Studies of Southern North Sea Herring

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Introduction

The herring otolith has become increasingly important in recent years as a racial character. Early research workers (JENKINS, 1902; LISSNER, 1925) mentioned the existence of differences in the otolith centres of spring and autumn spawning herring but EINARSSON (1951) was one of the first workers to recognize the full importance of the herring otolith for stock differentiation. He used the nucleus of the otolith to distinguish the different spawning types amongst Icelandic herring and was able to show that spring spawners were characterized by opaque otolith centres and autumn spawners by hyaline otolith centres. POSTUMA (1958) measured the size of the nucleus in summer/autumn spawning herring in the southern North Sea and found a significant difference between fish spawning on the Dogger, at Sandettié, and in the Channel. The most recent developments in this field, however, have been in the work of PARRISH and SHARMAN (1958, 1959), who used EINARSSON's technique to distinguish spring and autumn spawners by means of the otolith centre but were also able to show the presence of two distinct otolith types amongst summer/autumn spawning fish: "Those with a 'wide' first winter zone and a relatively small first growth zone and those with a thin-sharp or 'narrow' first winter zone and a relatively large first growth zone". They have been able to demonstrate the distribution of these types amongst adolescent and adult herring of the northern North Sea. This work has been followed up by DAS, POSTUMA, and ZIJLSTRA (1959), BOHL (1960) and RAITT (1959) who have all confirmed the presence of these otolith types amongst herring of the southern North Sea. The following paper is an account of the work on herring otoliths undertaken by the author at the Fisheries Laboratory, Lowestoft in 1958 and 1959 during the tenure of a Development Commission Fishery Research Training Grant.

Material and Methods

The present results are based on the examination of the otoliths from 10,866 herring. The majority of these were sampled from the North Shields,

Whitby, East Anglia, and Sandettié fisheries of 1958 and 1959. Further samples were obtained during the ICES international herring tagging experiment on the Bløden Ground in August 1958 and on surveys made by R.V. "Sir Lancelot" and the German research ship "Anton Dohrn" in October 1958. A number of samples collected during the Whitby and East Anglia fisheries of 1951, 1952, 1953, and 1954 were also made available to the author.

PARRISH and SHARMAN photographed all their otoliths and made their diagnoses and measurements of the first growth zone from photographic prints. Although a small collection of prints has been assembled at Lowestoft for reference purposes, the present results were all obtained by direct observation using a Bactil binocular microscope with a $\times 22{\cdot}5$ magnification. The otoliths were mounted in plastic resin, using the same method as PARRISH and SHARMAN (1959), and viewed on a black background by direct lighting from a high-intensity spot lamp.

In nearly all cases the otoliths were collected from routine biological samples so that data on length, sex, maturity stage, and vertebral count were also available for each fish and age and L_I data could be calculated from the scales. The identification of "narrow" and "wide" first winter rings on herring otoliths was found to be relatively easy and I am indebted to Mr. PARRISH and Mr. SHARMAN for the help they gave me at the start of these investigations.

Distribution of Otolith Types amongst I-Group Fish in Southern North Sea, Autumn 1958

Otoliths of young herring were collected during the ICES Bløden tagging experiment in August and during the "Anton Dohrn" Dogger Survey in October. Two of the August samples were from purse seine hauls made for tagging purposes, and two were from hauls made with the "Sir Lancelot's" Dutch herring trawl. The October samples were all taken with a Dutch herring trawl including some from a survey conducted by the "Sir Lancelot" in the Dogger Bight.

It was originally hoped that by plotting the percentages of "wide" and "narrow" types in the samples some idea might be obtained of their distribution in the southern North Sea, which might in turn throw some light on recruitment problems. Unfortunately herring were not caught at all the stations fished and there are large gaps in the picture (Fig. 1). However, two facts do stand out: —

1. That, east of the Dogger in the Bløden Ground area, in August and October 1958, the majority of I-group fish in the samples were "wide" types.
2. That in October, north-west of Dogger, there were large concentrations of I-group herring which were independently sampled by the Scots, Germans, and English and in all cases these were found to be predominantly of the "narrow" type (SCHUBERT and PARRISH, personal communication). It is interesting to note that the 1-ringers caught in the area of the Shields fishery from June to September were also without exception "narrow" ringed fish.

In Table 1 the mean lengths of "wide" and "narrow" type fish in each

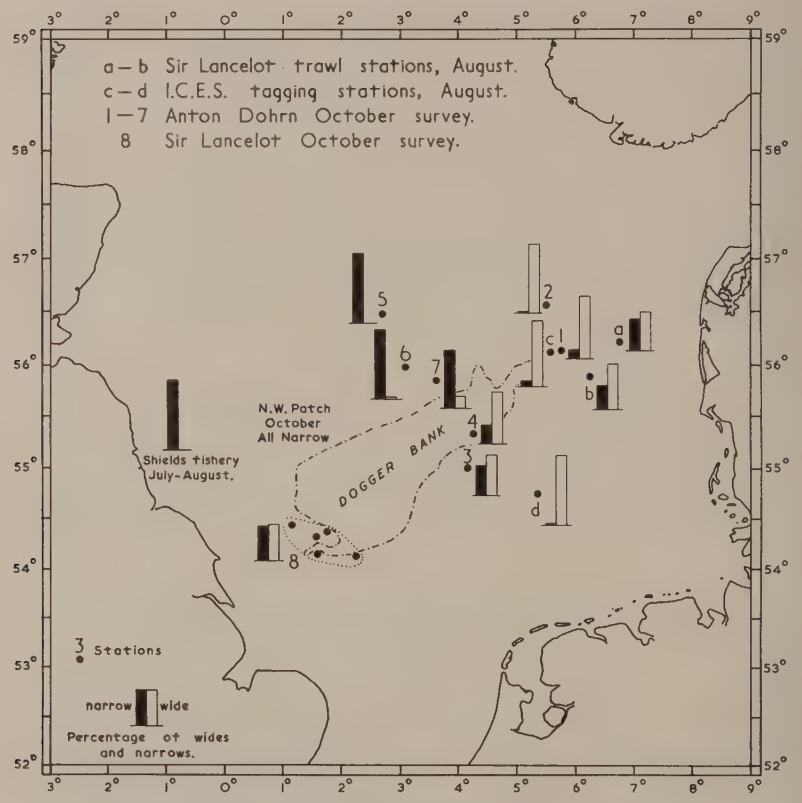

Figure 1. Distribution of I-group herring otolith types. October 1958.

Table 1

Otolith types and mean lengths of 1-ringers, 1958

Position	Stations (see Fig. 1)	All fish	Mean lengths (cm) "Narrow" type	"Wide" type	Difference between types (cm)
Bløden	a	17·1	18·0	16·3	1·7
Bløden	b	16·9	18·1	16·2	1·9
Bløden	c	16·4	–	16·3	–
South of Bløden	d	16·9	–	16·8	–
Bløden	1	17·9	–	17·6	–
Bløden	2	17·4	–	17.2	–
Clay Deep Area	3	19·2	20·5	18·5	2·0
Clay Deep Area	4	19·1	20·5	18·5	2·0
North-west Dogger	5	22·2	22·2	–	–
North-west Dogger	6	22·2	22·3	–	–
North-west Dogger	7	21·0	21·6	–	–
Dogger Bight	8	20·6	22·0	19·3	2·7

sample are compared with the total mean length. Care must be taken in interpreting these results, as several different fishing gears were used to collect the samples. However, despite this there is a clear length difference between "wide" and "narrow" fish in all samples, whether Dutch trawl or purse seine was used. The mean lengths of the Bløden samples are considerably smaller than those taken from the north-west Dogger area. The difference in length between "narrows" and "wides" is maintained throughout the length range from 16·4 cm to 22·2 cm, from the Bløden to the north-west Dogger. In all samples the bigger fish were further from the nursery area, and "wide" and "narrow" type fish appeared to be in separate areas. This could be a true separation of types down to an early stage on the nursery ground, or it could be a separation by size as the fish move across the nursery area. In either case different otolith types might well characterize different adult fisheries.

These results agree well with those of BOHL (1960) but the presence, in the samples, of an unusual otolith type, must also be noted. This "F" type, as it was subsequently called (RAITT, 1961), was characteristic of the 1956 year-class and its presence and importance as a biological tag have already been commented on.

Otolith Composition of East Anglian Samples 1951–1959

The percentage otolith composition of the different year-classes found in East Anglian samples from 1951 to 1954 and in 1958 and 1959 are shown in Table 2.

The numbers of fish examined in the years before 1958 were small but the overall results show two things: —

(i) That the percentages of "wide" and "narrow" type fish amongst the 3 year-old recruits from 1951 to 1959 vary considerably.

(ii) That year-classes maintain their identity from full recruitment. There is no trend visible, and the annual variation appears to be about 10%.

There is one exception to the homogeneity of year-classes and this is between the 5's of 1958 and the 6's of 1959. Here the ratio of "narrow" to "wide" is reversed. The explanation for this is not known but it may be due to inadequate sampling since the numbers of older fish were so small in these two years.

In 1958 the otolith type of the 3 year-olds in the East Anglian fishery differed markedly from the 4 year-olds. In this year 82% of the 3 year-olds were "narrow" type. This contrasts very sharply with the results PARRISH and SHARMAN (1959) obtained at East Anglia and Sandettié in 1957 where over 80% of the 3 year-old recruits they sampled were "wide" type. However, the results for the 4 year-olds in 1958 are close to those PARRISH and SHARMAN found for this year-class so that the 3 year-old result is probably a true difference between year-classes and not a difference in interpretation. Furthermore, the composition of the 4 year-olds in 1959 was almost identical with that of the 3 year-olds in 1958.

BURD (in press) has concluded, from the consistency of L_1 distributions within a year-class at East Anglia, that the Downs stock is homogeneous

Table 2

Percentage distribution of Narrow type (N) and Wide type (W) otoliths in samples at East Anglia, 1951–1959

	Age in years															
	3				4				5				6			
Year	N	W	?	No.	N	W	?	No.	N	W	?	No.	N	W	?	No.
1951	11	84	5	43	22	70	8	76	10	85	5	78	27	67	6	52
1952	6	94	–	84	3	94	3	34	19	81	–	32	–	100	–	25
1953	48	46	6	228	16	79	5	99	23	77	–	47	29	71	–	24
1954	58	35	7	168	43	51	6	125	9	87	4	79	15	75	10	20
1955																
1956	No samples															
1957																
1958	82	12	6	837	19	75	6	602	31	55	14	208	58	35	7	59
1959	38	57	5	1066	88	10	2	332	32	65	3	231	71	27	2	70

	Age in years								Total number of otoliths examined
	7				8 and over				
Year	N	W	?	No.	N	W	?	No.	
1951	23	70	7	30	31	60	9	45	324
1952	–	100	–	9	30	70	–	10	194
1953	11	89	–	35	17	83	–	41	474
1954	33	62	5	21	13	83	4	46	459
1955									
1956	No samples								
1957									
1958	45	52	3	33	25	72	3	36	1775
1959	76	20	4	25	31	64	5	39	1767

Table 3

Percentage distribution of Narrow type (N) and Wide type (W) otoliths in samples at Whitby, 1951–1959

	Age in years																Total number of otoliths examined
	3				4				5				6				
Year	N	W	?	No.	N	W	?	No.	N	W	?	No.	N	W	?	No.	
1951	90	4	6	171	–	–	–	–	–	–	–	–	–	–	–	–	171
1952	66	28	6	136	80	15	5	20	–	–	–	–	–	–	–	–	156
1953	97	3	–	99	65	30	5	95	100	–	–	15	–	–	–	–	209
1954	91	4	5	169	89	6	5	18	63	34	3	32	90	10	–	10	229
1955																	
1956	No Samples																
1957																	
1958	100	–	–	16	66	24	10	38	88	6	6	16	85	13	2	61	131
1959	60	35	5	549	95	2	3	58	73	24	3	30	87	13	–	54	665

Table 4

Otolith composition of 3 and 4 year-old fish, North Shields, 1958

Percentage otolith types in each month	3 year-olds			Number of fish examined	4 year-olds			Number of fish examined
	"Narrow"	"Wide"	Doubtful		"Narrow"	"Wide"	Doubtful	
June	96	2	2	97	35	56	9	68
July	94	5	1	137	46	49	5	104
August	88	6	6	34	58	38	4	24
September	89	7	4	100	59	34	7	131

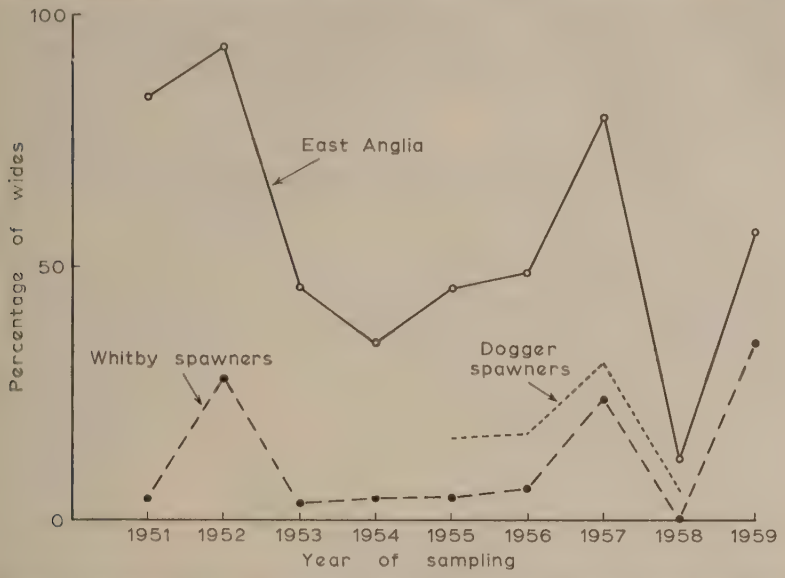

Figure 2. Percentage "wides" amongst 3 year-old recruits at Whitby, Dogger, and East Anglia 1951–1959.

from full recruitment. The results from the examination of the otolith types from 1951 to 1959 are in conformity with this, since the considerable differences found between year-classes were maintained year after year.

Otolith Composition of Whitby Samples, 1951–1959

The otolith composition of the different year-classes represented in the samples from the Whitby spawning fishery are shown in Table 3. The data refers to spawning or newly-spawned fish only.

The same points are again demonstrated. The percentage of "wides" and "narrows" in the 3 year-old recruits varies from year to year, and year-classes maintain their identity from full recruitment.

In Figure 2 the percentage of "wides" in the 3 year-old recruits at Whitby and East Anglia are plotted for the years 1951–1959. The figures for East Anglia, 1955, 1956, and 1957, are obtained from Das, Postuma, and Zijlstra (1959) and the figures for Whitby for these years are obtained from the otolith composition of the 6's, 5's, and 4's in 1958, these being fish of the same year-class as the 3's of 1955, 1956, and 1957. In addition figures for 3 year-old Dogger spawners taken from Das, Postuma, and Zijlstra (1959), for the years 1955 to 1958, are plotted. It can be seen that in the years when the East Anglian 3 year-olds were dominated by fish with "wide" type otoliths there was a corresponding increase in the percentage of "wides" amongst the Whitby spawners. The figures for 1952, 1957, and 1959 all show over 20%

"wide" types at Whitby. A corresponding rise amongst Dogger 3 year-olds can be seen in 1957. This is an interesting relationship between so-called "Banks" and "Downs" stocks, as defined by CUSHING and BURD (1957), and will be discussed later.

Otolith Composition of North Shields Samples in 1958 compared with those of other Adult Fisheries

Table 4 shows the results obtained from an otolith analysis by months of the samples from the North Shields fishery of 1958.

There is a marked year-class difference between the 3 and 4 year-old fish, the former being almost entirely "narrow" type while the latter show a varying mixture of "wides" and "narrows".

The 3 year-olds at North Shields are feeding intensively and will probably recruit, when mature, to several different spawning communities (BURD, 1958). These spawnings are separated spatially and temporally. The spawning off Whitby occurs about September, that on the Dogger in September and October, and the spawnings in the Southern Bight and Channel from November to January. BURD (1958) has shown that in July at North Shields (when there is the greatest range in the maturity stages) it is possible to distinguish between fish which are nearly ready to spawn (maturity stages IV and V) and those which will spawn later (stages I–III and III). A forecast of the number of recruits to East Anglia is made on the basis of the number of fish below maturity stage IV in these samples.

The otolith composition of the 3 and 4 year-olds in July 1958, split by maturities, is shown in Table 5.

The marked year-class difference observed over the whole fishery is even more obvious in the fish below maturity stage IV. The 3 year-olds, on which the 1958 forecast of 3 year-olds for East Anglia was based, were almost entirely of the "narrow" otolith type. The same year-class difference has already been demonstrated (Table 2) in the 1958 East Anglian samples.

In Table 6 the percentage otolith composition of the low maturity fish at North Shields in July is compared with that of the mature East Anglian fish and also with that of the spawning fish at Sandettié in November and December. The percentage of "narrow" and "wide" types in the different fisheries is very similar.

The mean lengths of the "narrow" fish in different year-classes throughout the whole of the North Shields fishery were significantly higher than those of the "wides" (Table 7). Thus, the bigger fish in any year-class were predominantly "narrows". The decrease in the percentage of "narrows" between North Shields and East Anglia and Sandettié is probably caused by the loss of some of the larger fish to earlier spawnings.

In Table 8 the otolith type compositions of the low and high maturity stage fish at North Shields in July are compared with those of Whitby and Sandettié spawners. The composition of the Whitby spawners was obtained from the stage VI fish in the September North Shields samples, which were from the area of the Whitby fishery.

The otolith composition of the 3 and 4 year-old fish, with low maturities in July, at North Shields, was very similar to that of Sandettié spawners and

Table 5

Otolith composition of samples split by maturity stages; North Shields, July 1958

Age (years)	Percentage otolith composition of fish below maturity stage IV			Percentage otolith composition of fish of maturity stage IV and over		
	"Narrow"	"Wide"	Doubtful	"Narrow"	"Wide"	Doubtful
3	93	5	2	100	–	–
4	32	63	5	72	22	6

Table 6

Relationship between the otolith composition of low maturity fish in July at Shields and that of the mature fish at East Anglia and Sandettié, 1958

	3 year-olds %			Number examined	4 year-olds %			Number examined
	"Narrow"	"Wide"	?		"Narrow"	"Wide"	?	
Shields, July 1958								
All fish under maturity stage IV	93	5	2	115	32	63	5	68
East Anglia								
All samples	82	12	6	837	19	75	6	602
Sandettié								
Spawning or recently spawned fish only	76	20	4	222	17	80	3	72

Table 7

Lengths (cm) of herring samples at Shields in 1958 by age and otolith types

Age (years)	Mean length (cm) at Shields, 1958	
	"Narrow" type	"Wide" type
3	24·4	23·3
4	26·9	25·5
5	28·1	27·2

Table 8

Relationship between otolith composition of low and high maturity fish at North Shields and that of spawners at Sandettié and Whitby

	3 year-olds					
	"Narrow"	"Wide"	Doubtful	"Narrow"	"Wide"	Doubtful
	Below stage IV			Stage IV and over		
Shields, July 1958	93	5	2	100	–	–
Sandettié spawners	76	20	4	–	–	–
Whitby spawners	–	–	–	100	–	–
	4 year-olds					
	Below stage IV			Stage IV and over		
Shields, July 1958	32	63	5	72	22	6
Sandettié spawners	17	80	3	–	–	–
Whitby spawners	–	–	–	66	24	10

Table 9

Otolith composition by months of 3 year-old herring, North Shields, 1959

	% "Narrow"	% "Wide"	% ?	Number of fish examined
May	55	35	10	85
June	52	41	7	153
July	51	43	6	226
August	67	28	5	293
September	57	37	6	374

the composition of the high maturity fish was very close to that of Whitby spawners.

Burd (1958; and in press) has shown the same general relationship, using the L_1 distributions of the 3 and 4 year-old fish in the different fisheries. There would appear then to be a very close relationship between L_1 and otolith type. This is discussed more fully in a later part of the paper.

Otolith Composition of North Shields Samples in 1959, compared with those of other Adult Fisheries

The results obtained from the North Shields fishery in 1959, although different from those of 1958, demonstrated the same general relationship with other fisheries. The otolith composition of the samples, by months, is shown in Table 9. Only the 3 year-olds recruits can be considered, as the 4 year-olds occurred in too small numbers. As in the previous year, no significant trend by months was observed, the recruit fish maintaining their percentage otolith composition throughout the season. The proportion of "wide" type otoliths was, however, much greater than in 1958.

When the July samples are split by maturities, as in 1958, and the otolith type composition of the low maturity fish is compared with that of mature fish at East Anglia and spawners at Sandettié, of the same age, a very close agreement is again found. This is shown in Table 10. This is also the case when the composition of the high maturity fish is compared with that of the Whitby spawners. The results of the otolith analysis for the two succesive years, therefore, support the conclusions reached by Burd (1958) that the East Anglian recruits are present as low maturity stage fish in the North Shields fishery in the summer.

Relationship between L_1 and Otolith Types

Parrish and Sharman (1958) found that in herring of the north-western North Sea "narrow" and "wide" type otoliths exhibited significant differences in the measurement of the first growth zone and that there was a close correlation between this and the L_1 calculated from scale measurements. A number of otolith growth zone measurements were made from photographs taken at the Lowestoft Laboratory, and these were compared with the L_1 measurement from the scales of the same fish. Figure 3 shows the relationship found. "Wide" type otoliths tend to be associated with a small first growth

Table 10

Relationship between the otolith composition of low and high maturity fish at North Shields and that of mature fish at East Anglia and spawners at Whitby and Sandettié

3 year-olds	Percentage otolith composition of fish below maturity stage IV			Percentage otolith composition of fish of maturity stage IV and over			Number of fish examined
	"Narrow"	"Wide"	?	"Narrow"	"Wide"	?	
Shields, July 1959	38	55	7	69	26	5	226
Whitby spawners	–	–	–	60	35	5	523
East Anglia	38	57	5	–	–	–	1066
Sandettié (spawning or recently spawned fish)	33	64	3	–	–	–	247

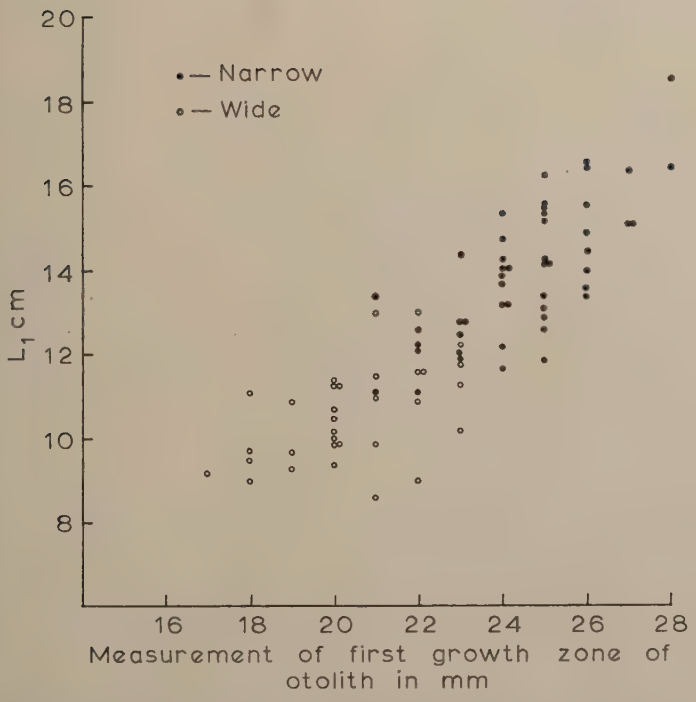

Figure 3. Relationship between L_1's and otolith measurements of "wide" and "narrow" type fish.

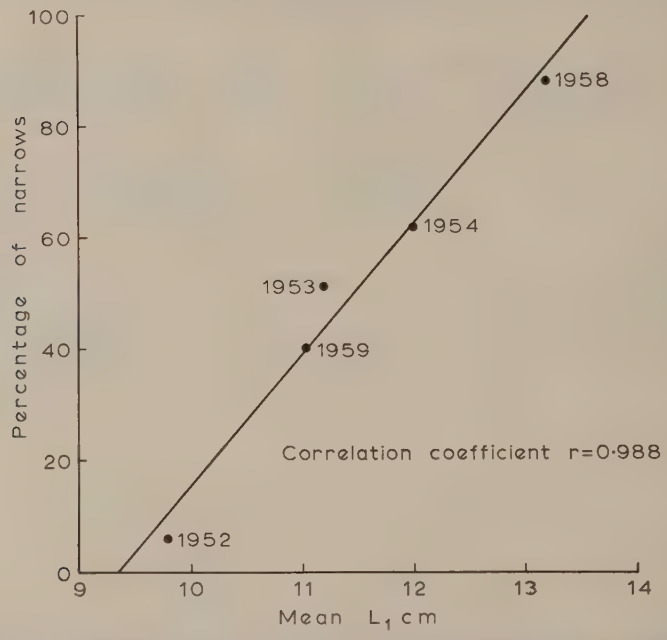

Figure 4. Percentage of "narrows" amongst 3 year-olds at East Anglia plotted against the mean L_1 of all 3 year-olds in each year sampled.

zone on the otolith and a small L_1, while "narrow" type otoliths tend to be associated with larger growth zones and larger L_1's.

Further evidence of the close relationship between the otolith composition of a year-class and the L_1 distribution can be seen in Figure 4. Here the percentage of "narrows" in the recruit 3 year-olds of 1952, 1953, 1954, 1958, and 1959 is plotted against the mean L_1 for 3 year-olds of the same year. The resulting regression is very good, allowing for the fact that the mean L_1 is not the best statistic for describing a non-normal distribution. The 1951 results could not be used in this figure as the numbers of 3 year-olds in the samples for that year were too small for an adequate measurement of the otolith composition.

As the herring population in the Southern Bight is a mixed one of two distinct otolith types, one of which is associated with a low L_1, calculated from the scale measurement and the other with a high L_1, it should be possible to split the population using the L_1's and obtain the same results as those given by an otolith type split (RAITT, 1959). The method used was the graphical one discussed by HARDING (1949) and subsequently used by CASSIE (1954) and SATO (1959). This method makes use of the fact that the cumulative percentage frequencies of a normal distribution lie on a straight line when plotted on arithmetic probability paper. When the L_1's of the "wide" and "narrow" 4 year-old fish at East Anglia in 1958 are plotted it can be seen (Figure 5) that their L_1 distributions approximate to normal curves. If now all the L_1's from

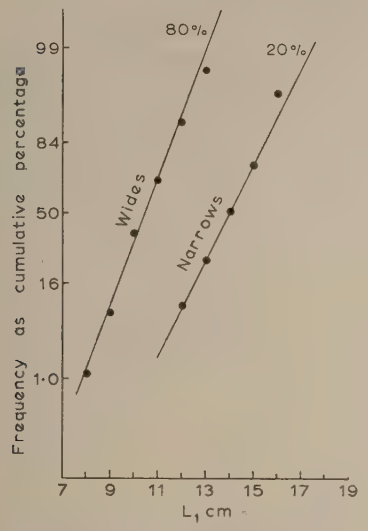

Figure 5. L_1 distribution of "wides" and "narrows" amongst 4 year-olds at East Anglia 1958.

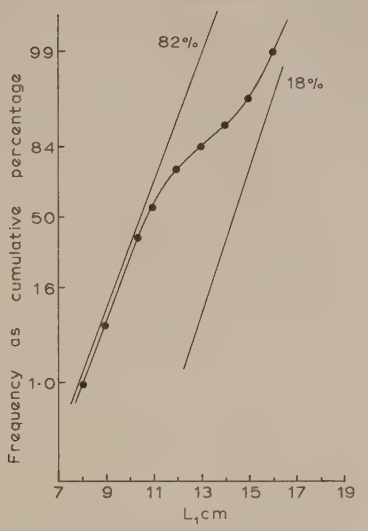

Figure 6. L_1 probability split of 4 year-old population at East Anglia 1958.

these fish are summed together and replotted the result is an S-shaped curve (Fig. 6). The point of inflexion of this curve is determined by eye and this gives the percentage split of the population. The original cumulative percentage frequencies are recalculated on the basis of the two component totals found and after suitable adjustments these points are found to fall more or less on two straight lines. The two straight lines represent two normal distributions and the means and standard deviations can be read off the graph. Otolith typing of the fish for which L_1's were calculated gave an 80/20 percentage mixture and a straight L_1 probability split gave an 82/18 percentage mixture. There is no overlap in the standard deviations of the two distributions.

This technique demonstrates the close relationship between L_1 and otolith type and it is likely that both are closely linked with growth-rates and feeding. The upper limit of the standard deviation of the "wide" type L_1 distribution occurs at 11·5 cm. The same result was obtained from all the year-classes examined in this way. This may well be a clue to the basic difference between "wides" and "narrows". It is known that young herring move off-shore into deeper water at a length of about 8 cm. Wood (1959), and Burd (1958) have shown that adolescent herring recruit to the North Shields feeding fishery at a mean length of 21·8 cm. It may be that the time at which a length of 11·5 cm is reached determines whether a fish becomes a "wide" or a "narrow". In other words, if a fish has not reached a size greater than 11·5 cm by its second winter, it may be bound to lay down a "wide" type ring. There are no data to support this hypothesis, however, and much work still has to be done to fully understand the methods of formation of the first winter ring in young herring.

Otolith Types and the Change in Recruitment to East Anglia

In the early 1950's there was an increase in the length for age of herring in the southern North Sea (ANCELLIN, 1953; GILIS, 1954; CUSHING and BURD, 1956). This was associated with a sharp increase in the numbers of *Calanus* over the period 1950–1955 (CUSHING and BURD, 1956). Before 1950, recruitment to East Anglia had been only partial at 3 years of age, full recruitment not occurring till a year-class was at least 4 or 5 years of age. It is believed that the increased feeding in the early 1950's resulted in the 3 year-olds increasing in size and therefore maturing earlier, so that recruitment was almost complete at 3 years of age from 1952 to 1956.

In the years prior to the growth change the 3 year-old recruits were the larger fish with big L_1's. In 1952 recruit 3 year-olds had low L_1's for the first time. These fish (1949/50 year-class) had increased feeding conditions in their second and third years, and full recruitment took place at 3 years of age. From Table 2 it can be seen that this year-class was composed almost entirely of "wide" type fish. The 1953 3 year-olds (1950/51 year-class), however, had improved feeding conditions all their lives. These fish show an increase in the percentage of "narrows", which is also found in the 1954 recruits. The results for the 1953 recruits show a 50/50 mixture of "narrows" and "wides", while those for 1954 show a slightly higher proportion of "narrows". There is a corresponding increase in the mean L_1 of the 3 year-olds in these two years.

Unfortunately no East Anglian samples are available for 1955, 1956, or 1957, but from the results obtained by DAS, POSTUMA, and ZIJLSTRA (1959) from the Sandettié fishery for those years it appears that the otolith compositions found for the 4's, 5's, and 6's of 1958 were representative of their year-classes. Table 2 shows that 1955 and 1956 were similar to 1953 and 1954 in the pattern of the recruits, but that in 1957 there was a sharp increase in the relative proportions of "wides". This high proportion of "wides" in the 1954/55 year-class was recorded by PARRISH and SHARMAN (1958) and was associated with a lower mean L_1 and a decrease in mean length.

We cannot use the older year-classes of 1951 to say what the otolith composition of the 3 year-olds was in pre-1950 years, as recruitment was only partial and the composition of a year-class would only be expected to be constant after full recruitment. From the mean L_1's for 3 year-old recruits in 1948, 1949, and 1950 (Table 11), however, we can estimate (using Figure 4)

Table 11

L_1's at East Anglia (After A. C. BURD)

Year-class	3 year-olds	4 year-olds	Difference	Mean difference
1945/46	11·37	10.56	0·81	
1946/47	12·15	10·32	1·83	1·18
1947/48	11·88	10·80	1·08	
1948/49	10·80	9·79	1·01	
1949/50	9·80	9·33	0·47	
1950/51	11·24	11·06	0·18	
1951/52	12·00	11·67	0·33	0·36
1952/53	12·80	12·52	0·28	
1953/54	11·80	11·23	0·57	
1954/55	11·00	10·70	0·30	

that their otolith composition was probably in the region of 55% "narrows" and 45% "wides". When full recruitment occurred at age 4, the 4 year-old recruits had small L_1's (Table 11) and were probably "wide" types. Since the number of 4's in any year was always greater than the number of 3's of the year before (HODGSON, 1958) and total recruitment occurred at 4, we can assume that fish with "wide" type otoliths predominated in the fishery up until 1950. Proof of this can be seen by examining the older age-groups in the 1951 samples (Table 2). These indicate that from 4 year-olds onwards about 70% of the fish in all year-classes represented had "wide" type otoliths. So the incidence of "narrows" in the fishery was small, the bulk of the recruits being "wide" types and only a small percentage of the 3 year-olds being "narrows".

From 1953 to 1956 recruitment was almost complete at 3 years of age because the mean length-for-age had risen. Table 11 shows that the mean L_1 of the 4 year-olds in these years was high. There were probably no fish with small L_1's recruiting at 4 years of age, and these would be the fish that one would expect to have "wide" type otoliths. CUSHING and BURD (1956) showed that, allowing for the advance in maturity there was a reduction in the numbers of older fish of from 25–50% in 1952–55 compared with the immediate post-war years. As the fully-recruited 3 year-olds of 1953–56 showed about 50/50 proportion of "wides" and "narrows", and the numbers of older fish were reduced, the East Anglian fishery in these years became relatively more dependent on "narrow" type fish.

The results for the 1958 East Anglian season must now be considered. It can be seen (Table 2) that the otolith composition of the 3 year-old recruits shows a higher proportion of "narrows" than in any year-class previously sampled. The otoliths are more like those of Bank recruits in that they have a very large first growth zone and a narrow first winter ring. Also the vertebral characters (56·42), mean length and L_1 distribution are much closer to those of Bank herring. It would seem that the 3 year-old recruits with low maturities at Shields in July, used as a basis for the forecast, did indeed turn up in the East Anglian fishery. BURD (in press) suggests that the recruitment pattern of recent years has broken down and that the generally low level of *Calanus* since 1956 is resulting in a return to the pre-1950 pattern of recruitment. From the otolith composition of the 1958 recruits it would seem that this low *Calanus* level had resulted in a delay in growth, giving Bank-type recruits at East Anglia, which might otherwise have recruited to Scottish fisheries three months earlier. The failure of the recruitment to the Scottish north-east coast fishery in the summer of 1958 may be further evidence of this.

In 1959 there was a small majority of "wide" type fish amongst the 3 year-old recruits to East Anglia. The 1959 season has been fully described by CUSHING (1960) who also suggests the possibility of a change in recruitment back to the pre-1950 pattern. The 3 year-olds showed a drop in mean length and were as small as those before 1950. They had, however, still spent one year in three under good feeding conditions, for there was rich *Calanus* in 1957 although in 1956, 1958, and 1959 feeding was poor. CUSHING goes on to say "the recruits came in two parts, part from Shields and part from elsewhere. The second part came very late into the fishery..." and he suggests that the next stage is that, with subsequent year-classes, this second part will recruit a year later, i.e., if the theories advanced so far are correct, as "wide" type 4 year-olds with small L_1's.

Discussion

(a) "Wide" and "narrow" otolith types in the Southern Bight

The biological significance of the "wide" and "narrow" otolith ring types is still very little understood. There is little doubt that it is not a year-class phenomenon and that it is probably diagnostic of conditions on a particular nursery ground; this being connected with the time of arrival on the nursery area. Bridger (1960), using the author's results for the otolith compositions at East Anglia, has suggested "that the abundance of the subsequent wide recruits to East Anglia is connected with the number of eggs laid in the Downs area".

It would seem that fish with "wide" type otoliths may be derived at least partly from spawnings in the Southern Bight. The mean lengths of the two types amongst young and old herring in 1958 showed that the "narrow" ringed fish were larger. Also it has been shown in an earlier section of the paper (p. 320) that high L_1's tend to be associated with "narrow" type fish. From this one would expect, given approximately the same growth conditions in the nursery areas, that "wide" type fish were the result of spawnings in late autumn and winter and "narrow" type fish came from spawnings in summer and early autumn. If the nursery ground was a common area, e.g. the Bløden Ground, the different times of spawning would bring the young fish on to the nursery area at different times and might well result in their experiencing different environmental conditions before formation of the first winter ring. "Wide" type recruits have never been found in substantial quantities amongst the 3 year-old recruits in the north-western North Sea (Parrish and Sharman, 1958) and it may be that the separation by time on the nursery ground prevents the winter spawned fish from mixing with the summer and autumn spawned fish. Under poor feeding conditions a delay in growth could result in "narrow" type fish recruiting to southern fisheries as they did to East Anglia in 1958.

The "wides" of the 1955/56 year-class did not recruit to East Anglia as 3 year-olds (Table 2) and it was expected that they might turn up as 4 year-old recruits in 1959, thus confirming a return to the split recruitment pattern of earlier years (Raitt, 1959). This was not the case, however, and indeed from the work of Parrish and Sharman (1959) and Das, Postuma, and Zijlstra (1959), in the north-western North Sea and Dogger respectively, it would seem that the "wide" type fish of this year-class have not been identified in any numbers from any North Sea fishery. If the hypothesis that Southern Bight spawners give rise to "wide" type recruits is correct then this would be evidence of a year-class failure from the Southern Bight spawning; indeed Bridger (1959) has already suggested, from the small number of larvae associated with the spawnings in 1955, that this might happen. Parrish and Sharman (1959) sampled this year-class as 1-ringers on the Bløden Ground in 1957 and found only one sample which contained a significant percentage of "wide" type fish.

Bridger (1960) has also suggested that it is the reduction in numbers of older fish which has been the cause of the low larval abundance in recent years, since the young fish spawn first and their larvae may hatch into barren water before the spring outburst of plankton in the English Channel. With the reduction in numbers of older fish and the subsequent failure of the November

fishery (CUSHING and BURD, 1957) the East Anglian season has become almost entirely concentrated on the 3 year-old recruits. Recruitment is therefore very critical and a second year brood failure which was not saved by an influx of "narrow" type recruits might well see the collapse of the fishery.

(b) Relationship between East Anglia and Whitby 3 year-olds

In Figure 2 it was shown that in the years when there was a majority of "wide" type 3 year-old fish at East Anglia (1952, 1957, and 1959), over 20% "wides" were found at Whitby. The latter is a fishery characterized in the other years investigated by almost 100% "narrow" types amongst the 3 year-olds. DAS, *et al.* (1959) also show that in 1957 there was a corresponding increase in the numbers of "wides" in the Dogger spawnings. This was the only one of the three years when sampling took place on the Dogger. It would seem that when there is a very good "wide" year-class its effect is felt in the recruitment to fisheries which normally do not receive a "wide" type recruit component. The Whitby and East Anglian fisheries undoubtedly consist of quite distinct herring populations and it has been shown that year-classes in these fisheries maintain their identity from full recruitment. It is interesting, therefore, to find this obvious relationship between the two fisheries in the otolith composition of the 3 year-old recruits. If, as seems likely, "wide" type fish are derived from spawnings in the Southern Bight, it would appear that in certain years quite considerable numbers recruit to spawning areas other than that in which they were born and in general, having once done this, return to spawn there for the rest of their lives.

Summary

The examination of herring otolith types in the southern North Sea has shown the following facts and relationships.

1. In the East Anglian and Whitby fisheries, year-classes maintain their otolith type compositions from full recruitment. This confirms the view that herring tend to return for spawning to the same area throughout their adult life.

2. The otolith composition of the low maturity fish at North Shields in July and the recruits to East Anglia and Sandettié later in the same year are in close agreement, thus supporting BURD's (1958, and in press) method of forecasting the recruitment to the East Anglian fishery and also his finding using L_1 distributions.

3. The scarcity of "wide" type recruits from the 1955/56 year-class has been demonstrated and the possibility of a year-class failure discussed.

4. Evidence has been presented which points strongly to the theory that "wide" type recruits are at least partly the result of late spawnings in the Southern Bight.

5. The connection between the otolith composition of the 3 year-old recruits to East Anglia and to Whitby and the Dogger shows that when there is a strong "wide" type year-class a significant quantity turn up to spawn with the "Banks" fish.

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Some Unusual Otolith Types on the Bløden Ground in 1958 and their Subsequent Occurrence in the Adult Fisheries

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Introduction

Considerable emphasis has recently been placed on the herring otolith as a racial character. The discovery of "wide" and "narrow" first winter zones in the herring of the north-western North Sea (PARRISH and SHARMAN, 1958) has led to further research in other areas, e.g. Dogger Bank (DAS, POSTUMA, and ZIJLSTRA, 1959; and BOHL, 1960); Southern Bight (DAS, *et al.*, 1959; and RAITT, 1959). In the course of studies of the otoliths of adolescent herring from the Bløden area in 1958, and from the Southern Bight and North Shields area in 1959, the author observed the occurrence of unusual "double" first zoned otoliths amongst members of the 1956 year-class in these areas. This report deals with the results of the analysis of this material, and of some Scottish material from the north-western North Sea.

Material and Methods

The otoliths were collected from herring on the Bløden Ground and Dogger Bank area in August 1958 during the ICES herring tagging experiment, and cruises in October by the research vessels "Sir Lancelot", "Clupea", and "Anton Dohrn". One sample in November came from a commercial drifter catch. The year-class was also sampled during the North Shields and East Anglian fisheries of 1959 while the author was at the Fisheries Laboratory, Lowestoft. More recently, otoliths of herring from the Buchan pre-spawning and spawning fisheries of 1959 have been examined at the Marine Laboratory, Aberdeen.

The measurements of the Bløden samples were made from photographs enlarged to the same scale as those in the library of otolith photographic prints at the Aberdeen Laboratory. All other otolith growth zones were measured using the ocular scale in a Beck binocular microscope fitted with $\times$ 10

eyepieces and a 49 mm objective. This gave a magnification of approximately × 25. A scale was calculated for converting "ocular" units to "photographic" units so that all measurements would be comparable with those already published by PARRISH and SHARMAN (1958). All measurements recorded in this paper are therefore in "photographic" units.

Description

The fish sampled on the Bløden Ground in August 1958 were young herring, and from the length distribution (14–19 cm) they would seem to be I-group fish, caught at the end of their second summer, and typical of the age-group upon which the autumn Bløden fishery is based (BERTELSEN and POPP MADSEN, 1954, 1956, 1957; POPP MADSEN, 1959, 1960). Some of them, however, had two distinct winter zones on their otoliths. This type is illustrated in Figure 1 c and will be referred to as the "F" type otolith. These otoliths are quite different from normal "wide" and "narrow" type otoliths and from the more common type of "double" zoned otolith. These are illustrated in Figures 1 a, b, and d. The "F" type otolith is characterized by alternate "wide" and "narrow" hyaline zones between the nucleus and the edge. In assessing the age of these fish the question arises whether one of the rings is "false" and the fish belong to the I-group, or whether both are true winter zones and the fish are members of the II-group. In Table 1 the otolith measurement of the "F" types are compared with those of the "double ringed" types. They are shown to be quite different except in the growth zone measurement to the end of the second ring which is very similar in both types. The measurement to the end of the first growth zone in the "F" types is very small: much smaller than any measurement of first year's growth recorded by PARRISH and SHARMAN (1959).

The mean length of the "F" types, on the other hand, does not differ significantly from that of the "wide" and "narrow" type fish in the samples; it lies somewhere between them, as can be seen from Table 2.

Thus, from the data available, it seems likely that the first "wide" zone on the "F" type otoliths is a "false" or check zone laid down during the first year's growth period, and that the herring of this type sampled on the Bløden Ground in 1958 were I-group members of the 1956 year-class. On this basis, the phenomenon provides a useful biological tag.

Table 1

Comparison of growth measurements in "F" and double ring type otoliths

(Measurements in "photographic units")

Bløden Ground 1958	Growth measurement to 1st ring		Growth measurement to 2nd ring		Differences in two measurements		Number of fish
	Range	Mean	Range	Mean	Range	Mean	examined
"F" types	12–19	**14·66**	18–25	**21·78**	5–9	**7·07**	27
Double ring types.....	14–20	**17·12**	17–23	**20·71**	2–5	**3·56**	34

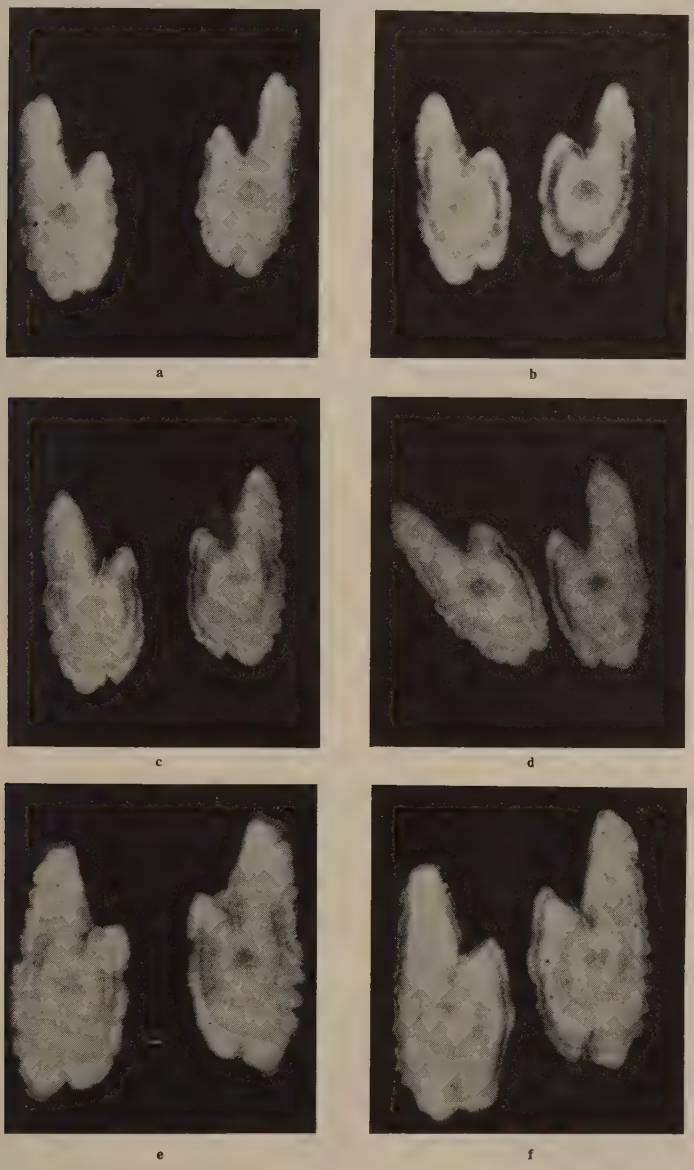

Figure 1. Photographs of some otolith types in herring. For full explanation, see text. a. "Narrow" type, I-group, Bløden 1958. – b. "Wide" type, I-group, Bløden 1958. – c. "F" type, I-group, Bløden 1958. – d. "Double ring" type, I-group, Bløden 1958. – e. "F" type, II-group, Buchan 1959. – f. "F" type, III-group, Buchan 1960.

Table 2

Mean length of "F" types compared with other fish in the same sample

Bløden Ground 1958	Mean length (cm)	Range (cm)
"F" type	17·06	14–18
"Narrow" type	17·97	16–20
"Wide" type	16·43	14–18
All fish	16·82	14–20

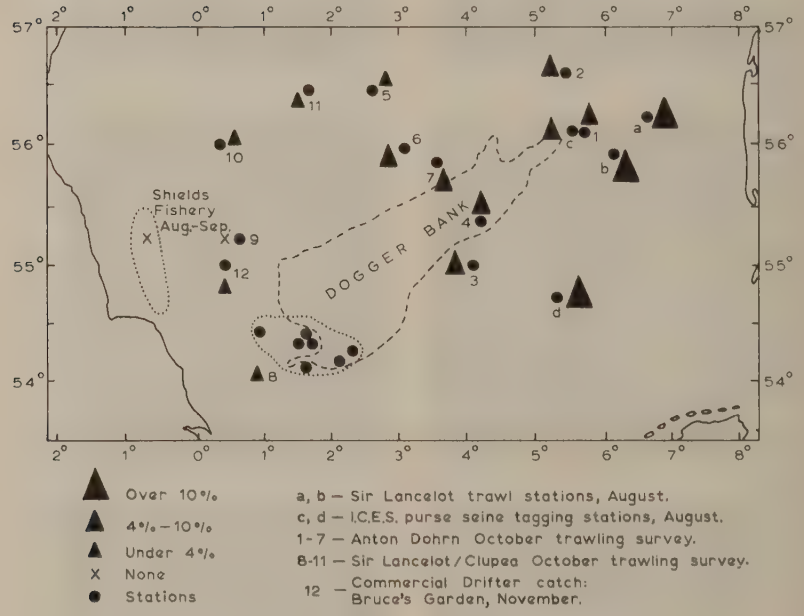

Figure 2. Distribution of "F" type otoliths. I-group, autumn 1958.

Table 3

Occurrence of "F" types, I-group, autumn 1958

Area	Number of fish examined	Number of "F" types	Percentage "F" types
Bløden Ground (Stations a, b, c, d, 1, 2)	556	62	11·2
East Dogger (Stations 3, 4, 6, 7)	295	20	6·8
West and north-west Dogger (Stations 5, 8, 9, 10, 11, 12)	444	10	2·3
North Shields fishery	37	–	–

Occurrence in I-Group, 1958

Adolescent herring were sampled on the Bløden Ground, Dogger Bank, and adjacent areas in the autumn of 1958. The distribution of "F" types amongst the I-group in this region is shown in Table 3 and Figure 2. Despite the difference in gears used by the different sampling vessels these data show that the majority of the "F" type fish were situated on the Bløden Ground and East Dogger regions; very few were found west and north-west of the Dogger and off North Shields. In one sample from the Bløden area 20% of the otoliths examined were of this type.

Occurrence in II-Group, 1959

Table 4 shows the percentage occurrence of "F" types amongst members of the 1956 year-class in the North Shields, Whitby, Buchan, Shetland, East Anglian, and Sandettié fisheries of 1959 and Table 5 gives the measurements of their first growth zones. Table 5 shows clearly that the ranges, and means, of the measurements are all similar, and agree well with those of the I-group in 1958.

In samples from the North Shields summer fishery about 5% of the fish examined were "F" types, and the same proportion was found amongst the spawners at Whitby in September. Samples from Buchan, collected from May

Table 4

Occurrence of "F" types, II-group, 1959

Area	Number of fish examined	Number of "F" types	Percentage "F" types
North Shields (May-August)..... 19 samples	705	36	5·1
Whitby (September)..... 12 samples	461	24	5·2
Buchan (May-September)..... 67 samples	2,862	46	1·6
Shetland (June-August)..... 12 samples	331	0	0
East Anglia (October-November).. 29 samples	1,066	22	2·1
Sandettié (November-December).. 6 samples	208	4	1·9

Table 5

Growth measurements of "F" types from I- and II-group herring

(Measurements in "photographic units")

	Growth measurement to 1st ring		Growth measurement to 2nd ring		Differences in two measurements		Number of fish examined
	Range	Mean	Range	Mean	Range	Mean	
I-group, 1958.....	9–19	**14·10**	16–25	**21·26**	5–12	**7·19**	62
II-group, N. Shields and Whitby 1959	11–18	**14·47**	19–25	**21·72**	5–10	**7·33**	60
II-group, East Anglia and Sandettié 1959	11–16	**13·32**	18–25	**21·32**	6–10	**8·00**	22
II-group, Buchan 1959.....	11–19	**14·54**	19–27	**22·35**	6–10	**7·80**	46

to September, showed that 1·6% of the fish were of this type. No significant trend by months could be seen but the majority were in the low maturity stages, suggesting that they would not, in fact, spawn in this area. There were no "F" types in the Shetland samples. About 2% turned up amongst the East Anglian samples in October and November, and amongst the spawners at Sandettié a month later.

To sum up, then, fish of the 1956 year-class, with the "F" otolith type, made up about 10% of the samples from the Bløden Ground in 1958, and the following year were found as 5% of the samples from North Shields and Whitby, and as 2% of those from Buchan, East Anglia, and Sandettié. Its occurrence amongst spawners was confined to Whitby and Sandettié. A few fish bearing this characteristic have subsequently turned up in the 1960 Buchan fishery. The otoliths from one of them can be seen in Figure 1 f.

Discussion

Hempel and Treckel (1959) record that in young fish (9–13 cm) sampled in August 1958 from German coastal waters, considerable difficulty was experienced in ageing the fish from the otoliths and they describe intermediate forms between "wide" and "narrow" types which seem not unlike the "F" type found in the present investigation. They suggest that the different ring structure may be due to the unusual feeding conditions of the estuaries. Popp Madsen (1959) recorded "unusually dense concentrations of 0-group herring of the 1956 year-class in the German Bight and along the Jutland coast" in the summer of 1957. He has also stated (personal communication) that they were not feeding when sampled (July), and soon afterwards moved offshore. It would seem that other workers have found a similar characteristic and their data would suggest that feeding conditions may be responsible for differences in ring formation but, as yet, zone types in herring otoliths cannot be ascribed purely to environmental influences.

The "F" type otolith, however, has only been found so far in the 1956 year-class and therefore may be of considerable importance as a biological tag. Observations on the distribution of this type may be a valuable index of the distribution of the 1956 year-class in later years. It will be useful, even if the numbers of "F" types are small, to see

(1) if the year-class extends its range with age, and

(2) if its numbers become relatively more abundant amongst the spawners in the north-western North Sea.

Summary

1. Amongst I-group herring sampled on the Bløden Ground in August 1958 there were some fish which had two winter zones on their otoliths. From the lengths and otolith growth zone measurements these were assigned to the I-group of the 1956 year-class and the otolith type was referred to as an "F" type.

2. The subsequent occurrence of these otolith types amongst adolescent and adult herring fisheries is described and its significance as a biological tag is discussed. Observations on the distribution of this type may be a valuable index of the distribution of the 1956 year-class in later years.

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The Experimental Modification of Meristic Characters in Herring (*Clupea harengus* L.)

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Introduction

The plasticity of meristic characters in fish under the influence of the external environment is now well known. Meristic counts have been shown to vary with such factors as temperature, salinity, and light conditions during early life. The experimental evidence has been reviewed by TÅNING (1952), while both the experimental and circumstantial evidence, with special respect to the herring, has been reviewed by BLAXTER (1958).

A number of recent papers should be mentioned to bring these reviews up-to-date. Some further experiments have been done on marine fish, a section of work which has been rather neglected in the past due to the greater difficulty of rearing them. MOLANDER and MOLANDER-SWEDMARK (1957) reared plaice and found that the mean vertebral count increased at incubation temperatures above and below 8°C. (This may be called the "Tåning effect.") ITAZAWA (1960) found a "Tåning effect" in *Channa argus*, the mean vertebral count increasing at incubation temperatures above and below 22–25°C. He also found a strong parental effect on the vertebral counts. MCHUGH (1954) working on *Leuresthes tenuis* and LINDSEY (1958) on *Oncorhynchus nerka* found that the light conditions during incubation also affected the mean vertebral count.

Of particular relevance to the plasticity of the meristic characters in *Clupea harengus* is some post-war work. BÜCKMANN (1950) and BÜCKMANN and HEMPEL (1957) in accordance with MCHUGH's (1942) findings on the offspring of *Clupea pallasii* correlated the mean vertebral count of herring larvae caught near the German coast with temperature at the spawning time and found a negative correlation. DAY (1957) described a similar correlation in adult herring off the Canadian coast.

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Some experimental work has been done on herring. The larvae are difficult to rear to the stage where vertebrae are formed and although this has been done by a number of workers (MEYER, 1878; SCHACH, 1939; DANNEVIG, 1948; and DANNEVIG and HANSEN, 1952) no strict temperature control was maintained nor have any counts of vertebrae been published. KOTTHAUS (1939) suggested that myotome counts would be correlated with vertebral counts and could be substituted for them. Both HEMPEL (1953), working on German coastal herring from Cuxhaven, and BLAXTER (1957) on Scottish east and west coast herring have counted the myotomes of larvae soon after hatching and found negative correlations between temperature of incubation and mean myotome count. HEMPEL reported mean myotome counts rather lower than those of Scottish herring and also lower than those of the larvae of German coastal herring given later in this paper. He used a different counting technique in which the myotomes in the extreme caudal region were not detected.

As the results of a joint investigation between the authors of this report at the Biologische Anstalt, on Helgoland in 1960, further experimental evidence of the plasticity of the meristic characters in herring is now available. Myotome counts have been obtained from larvae reared under different conditions of temperature and salinity. By rearing larvae beyond the yolk-sac stage, in a few cases to metamorphosis (see BLAXTER and HEMPEL, 1961), later meristic counts have also been obtained.

In addition to this work, other data on meristic counts obtained in Aberdeen by the second author in 1957 are also given.

Methods

Apparatus

In the Helgoland experiments, eggs and sperm were obtained by dissecting the gonads from spring spawning herring caught in the approaches to Kiel Harbour and near Cuxhaven at the mouth of the Elbe. These gonads were stored in jars (see BLAXTER, 1955) at about 4°C and taken by ship to Helgoland where the eggs were artificially fertilized. Additionally deep-frozen sperm obtained from a Clyde spring spawning herring were used for cross fertilizations. The eggs were incubated in different ways which are described in detail by BLAXTER and HEMPEL (1961).

1. The eggs were incubated in circulated water at different temperatures in 120 litre tanks. They were kept in darkness until hatching, the hatched larvae then being kept in artificial light. The mean temperatures with standard deviations are given in Table 2.

Some further eggs were incubated in 100 litre tanks in daylight. These tanks had a variable water circulation and no strict temperature control.

A "temperature shock" experiment was also done in which a series of plates of eggs were kept at 10°C, but each day one plate was transferred to 4°C for 24 hours.

2. Further fertilized eggs were incubated in 2 litre glass jars in different salinities from 5–50‰, but in a constant temperature of about 10°C.

3. Larvae from experiments done in Aberdeen prior to the Helgoland work were treated in the way described by BLAXTER (1961).

Table 1

Details of experiments

Parents with length in cm and vertebral count*	Date of fertilization	Experiments
Cuxhaven ♂ (1) × Cuxhaven ♀ (1) 27·4, 56 25·0, 56	26. Apr. 60	Different temperatures, about 5, 8, 11, 14°C
Cuxhaven ♂ (2) × Cuxhaven ♀ (2) 25·0, 57 25·5, 56	26. Apr. 60	Different salinities 5–50 ‰
Cuxhaven ♂ (3) × Cuxhaven ♀ (3) 26·5, 56 29·3, 55 25·5, 56	29. Apr. 60	Temperature shock experiment
Kiel ♂ (1) × Kiel ♀ (1) 24·0, 57 25·3, 56 Clyde	29. Apr. 60	Different temperatures, about 5, 8, 11, 14°C
(Scotland) ♂ × Kiel ♀ (1) 27·3, 57 25·3, 56	29. Apr. 60	Different temperatures, about 5, 8, 11, 14°C

* The numbers of the parents in brackets are the same as in Table 1 (BLAXTER and HEMPEL, 1961).

Sampling

Samples were taken of 50 larvae from the different experiments (a) when 50% had hatched and (b) at the end of the yolk-sac stage, which was taken to be about 60 day degrees (taking biological zero as −1°C) after 50% hatching. The larvae were anaesthetized in 2% urethane in sea water and fixed in 2% formalin. Larvae at later stages of development were removed from the tanks when they became moribund. They were also fixed in 2% formalin, but no urethane was used.

Table 2

Significance of myotome counts at different temperatures

Parents (date of fertilization)	Mean incubation temperature (°C)	Standard deviation	Mean myotome count and S. E. (with number in sample)	Variance ratio	Level of probability
Kiel ♂ × Kiel ♀ 29. April	4·51	± 0·68	61·20 ± 0·125 (50)	13·72 3 and 383 d.f. (temperature effect)	P < 0·001
	7·46	± 0·54	61·02 ± 0·125 (50)		
	10·76	± 0·36	60·67 ± 0·128 (48)		
	14·38	± 0·63	60·52 ± 0·125 (50)		
Clyde ♂ × Kiel ♀ 29. April	4·51	± 0·68	61·60 ± 0·125 (50)	10·26 1 and 383 d.f. (parental effect)	P < 0·01
	7·46	± 0·54	61·04 ± 0·125 (50)		
	10·76	± 0·36	61·14 ± 0·125 (50)		
	14·38	± 0·63	60·70 ± 0·135 (43)		
Cuxhaven ♂ × Cuxhaven ♀ 26. April	5·15	± 1·20	61·36 ± 0·132 (50)	3·06 3 and 182 d.f.	P < 0·05
	7·56	± 0·50	* 61·40 ± 0·132 (50)		
	7·75	± 0·40			
	10·86	± 0·34	61·24 ± 0·132 (50)		
	13·70	± 1·16	60·83 ± 0·155 (36)		

* Eggs incubated in two tanks for first nine days.

Counting of meristic characters

The myotomes of all larvae were counted under a binocular microscope using polarized light. The older larvae were stained with alizarin using TÅNING's (1944) technique (but without bleaching) for counting vertebrae and fin rays.

In all cases an attempt was made to count the number of *whole* myotomes. In the caudal region the myotomes may be indistinct and in order to avoid bias the samples were counted, usually without knowing their origin, by two observers. While one counted the myotomes of half the sample, the other one checked which was the last myotome. The observers changed over for the second half of each sample. Some samples were later recounted. When this was done it was found that the means obtained in repeat counts agreed closely (within 0·1) with those of the original counts, only with larvae at hatching. At the end of the yolk-sac stage there were sometimes differences between original and repeated counts, though in this case the trend was usually the same, i.e., a high or low count was confirmed by a high or low recount. The difficulty of getting agreement between counts at the end of the yolk-sac stage is probably due to the larvae becoming starved and the tails thin, with a resultant loss in clarity of the myotomes. The results of these counts are not given here for this reason. It would be worth noting in any future work that counts of myotomes at hatching are the more satisfactory.

The number of myotomes in the very young larvae was greater than the number of vertebrae that might have been expected, by 5–9 myotomes. In the older larvae, once the tail had turned up at about 16 mm length, it was possible to count the number of myotomes which positioned the vertebrae themselves, because at this stage the urostyle is partly formed. These counts are therefore termed "vertebral myotomes" as they should be the same as the future number of vertebrae. In still older larvae, over 22–24 mm in length, and including those that reached metamorphosis, it was possible to count some or all of the vertebrae themselves.

Design of experiments

Larvae from the crosses shown in Table 1 were sampled in these experiments for counts of meristic characters.

Results

Myotome counts

1. Effect of temperature

The mean myotome counts of larvae at hatching after incubation in different temperatures are shown in Figure 1. It will be seen that there is a general negative correlation between temperature and mean myotome count. Analyses of variance showed that there were significant differences between the mean myotome counts at the different temperatures (see Table 2).

2. Effect of salinity

The mean myotome counts of larvae at hatching from eggs fertilized and hatched in different salinities are shown in Figure 2. There were two sets of

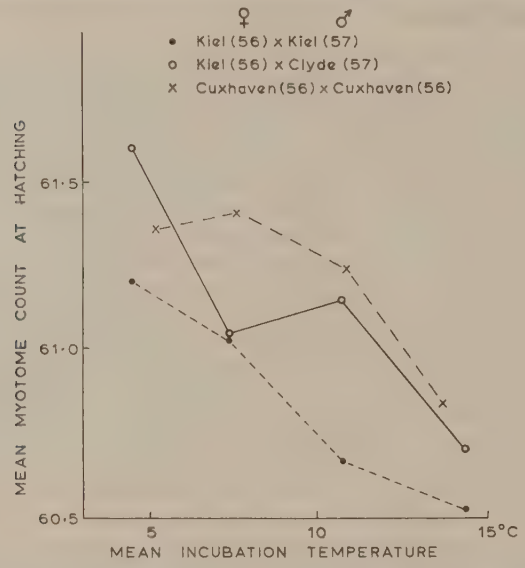

Figure 1. Showing the effect of incubation temperature on mean myotome count.

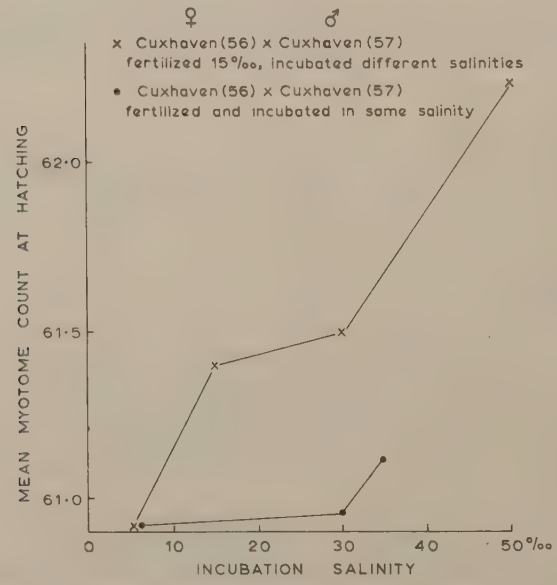

Figure 2. Showing the effect of incubation salinity on mean myotome count.

experiments using the same parents. In one set the eggs were fertilized at 15 ‰ and then transferred to salinities of 5, 15, 30, and 50 ‰. In the other, which was less complete, the salinity at fertilization and later salinities were the same, viz. 5, 30, and 35 ‰. In this experiment the hatching rate was lower and two of the samples taken were necessarily poorer. This could account for the lower values found.

There was a general positive correlation between salinity and myotome count in both experiments. Analyses of variance (Table 3) showed that only in the first was this significant.

Table 3

Significance of myotome counts at different salinities (temperature constant at 10°C)

Parents	Incubation salinity (with fertilization salinity) (‰)	Mean myotome count and S. E. (with number in sample)	Variance ratio	Level of probability
Cuxhaven ♂ × Cuxhaven ♀ 26. April	5 (15)	60·92 ± 0·122 (50)	20·28 3 and 196 d.f.	$P < 0{\cdot}001$
	15 (15)	61·40 ± 0·122 (50)		
	30 (15)	61·48 ± 0·122 (50)		
	50 (15)	62·24 ± 0·122 (50)		
Cuxhaven ♂ × Cuxhaven ♀ 26. April	5 (5)	60·92 ± 0·113 (39)	0·64 2 and 111 d.f.	not significant
	30 (30)	60·96 ± 0·100 (50)		
	35 (35)	61·12 ± 0·141 (25)		

3. Effect of length and growth in the yolk-sac stage

Although details will not be given here, there was no obvious correlation between length of larvae and their myotome counts within any one sample. Comparing the data on mean length (Blaxter and Hempel, 1961, Fig. 4) and mean myotome counts at hatching in temperature experiments a positive correlation between size and myotome counts is obvious. In contrast to this the salinity experiments yielded a negative correlation between length and myotome counts: the larvae reared at 50 ‰ were the smallest but had the highest number of myotomes. During the yolk-sac stage there was a general "addition" of visible myotomes with growth in length – the mean myotome count at hatching being lower than at the end of the yolk-sac stage. This "adding on" is presumably due to the myocommata in the extreme caudal region becoming visible in polarized light after hatching.

4. Effect of race and parents

It was also intended to use the myotome counts to test whether the meristic characters of the offspring were dependent on the vertebral counts of the parents or of the race as a whole. Blaxter (1957) found no significant racial or parental effect on the myotome counts of offspring from Clyde × Clyde, Clyde × North Sea (Banks), and North Sea × North Sea herring. The data reported here give no clear answer to this question.

(*a*) *Racial effect.* The mean vertebral counts of the Kiel and the Cuxhaven herring races are about 55·4; the mean count of the Clyde herring race is about 57·0. The cross fertilization experiments were done with the following parents (individual vertebral count in brackets): —

$$\text{Kiel } ♀ (56) \times \begin{cases} \text{Kiel } ♂ (57) \\ \text{Clyde } ♂ (57) \end{cases}$$

The hybrid larvae (Kiel × Clyde) had mean myotome counts which were significantly higher ($P < 0{\cdot}01$) than the control larvae (Kiel × Kiel) at all temperatures used. This difference might be a measure of the effect due to the males. Unfortunately there is no Clyde × Clyde control (due to the difficulty of storing eggs) reared under the same conditions with which to make a comparison. The only Clyde × Clyde myotome counts available are those of BLAXTER (1957) and the rearing conditions he used (other than temperature) were rather different, so that a fair comparison can not be made with the Helgoland results.

In contrast to the above it is striking that the mean myotome counts of the larvae from the Cuxhaven × Cuxhaven experiments are higher in nearly all cases than both Kiel × Kiel and even Kiel × Clyde larvae, in spite of the similarity of the vertebral counts of the Kiel and Cuxhaven herring groups. It should be mentioned that the larvae from the Cuxhaven experiments were considerably larger at hatching than the Kiel larvae (BLAXTER and HEMPEL, 1961).

(*b*) *Parental effect.* Comparison of the Kiel × Kiel and Cuxhaven × Cuxhaven crosses gives some evidence that the actual counts of the individual parents are unimportant in the determination of the metamerism in their offspring. Thus, while the Cuxhaven × Cuxhaven herrings both have 56 vertebrae and the Kiel × Kiel herrings 56 and 57, the Cuxhaven offspring have higher mean myotome counts. Clearly a very elaborate set of experiments would be required to test this further.

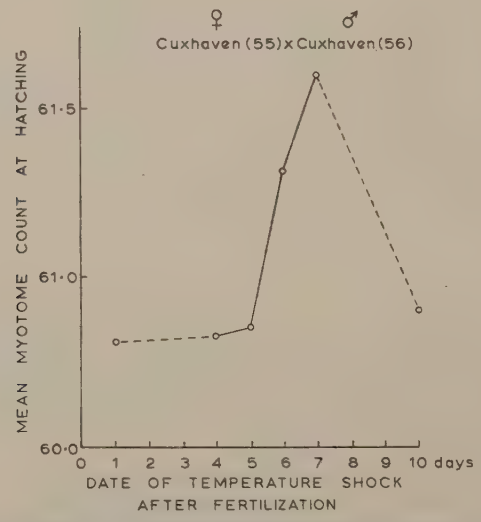

Figure 3. Showing the effect of a temperature shock (transferring from the usual temperature of 10°C to 4°C for 24 hours at different times after fertilization).

Table 4

Mean myotome counts in temperature shock experiment (Cuxhaven ♂ × Cuxhaven ♀, 29. April 1960)

Days after fertilization when shock given	Mean myotome count and S.E. (with number in sample)	Variance ratio	Level of probability
1	60·81 ± 0·134 (36)		
2	No sample		
3	No sample		
4	60·82 ± 0·127 (40)		
5	60·85 ± 0·180 (20)	6·59*	P < 0·001
6	61·32 ± 0·161 (25)	5 and 191 d.f.	
7	61·60 ± 0·117 (47)		
8	No sample		
9	No sample		
10	60·90 ± 0·149 (29)		

* A "t" test between the pooled results of days 1, 4, 5, and 10 against days 6 and 7 gives t = 5·55 (d.f. = 191) P < 0·001.

5. Effect of temperature shock

The results are shown in Figure 3 and Table 4. It will be seen that only a cold shock given 6–7 days after fertilization resulted in an upward trend in the mean myotome count. The level of myotome count before and after this period was about what might be expected for eggs incubated at 10°C (the usual temperature of the experiment) while the level of the myotome count at 6–7 days shock was what might be expected for eggs incubated at 4–5°C (the temperature of the shock). This upward trend is significant. It appears therefore that there is a particular sensitive period during incubation when the number of myotomes is susceptible to the effects of abrupt lowering of temperature.

Later meristic counts

1. Fin rays

After the end of the yolk-sac stage, counts were made of dorsal and anal fin rays once these became stainable with alizarin. However, it was seen immediately that the number gradually increased with growth and as it was not apparent when the final number had been reached, the results of these counts are not given.

Table 5

Counts of vertebrae and "vertebral myotomes"

Parents	Incubation temperature °C	Number of vertebrae 53	54	55	56	57	58	59	60	Total	Mean and S.E.	Variance ratio or "t"	Level of probability
German Coastal Herring 1960 racial mean vertebral count ≏ 55·4	8	–	–	6	2	–	–	–	–	8	55·25 ± 0·237	3·86 2 and 34 d.f.	P < 0·05
	11	–	4	10	1	–	–	–	–	15	54·80 ± 0·173		
	14	2	5	6	1	–	–	–	–	14	54·43 ± 0·179		
Clyde Herring 1957 racial mean vertebral count ≏ 57·0	7	–	–	–	–	–	6	7	1	14	58·64 ± 0·192	t = 2·10 70 d.f.	P < 0·05
	11	–	–	–	–	8	34	13	3	58	58·19 ± 0·094		
	15	–	–	–	–	–	1	–	–	1	58·0		

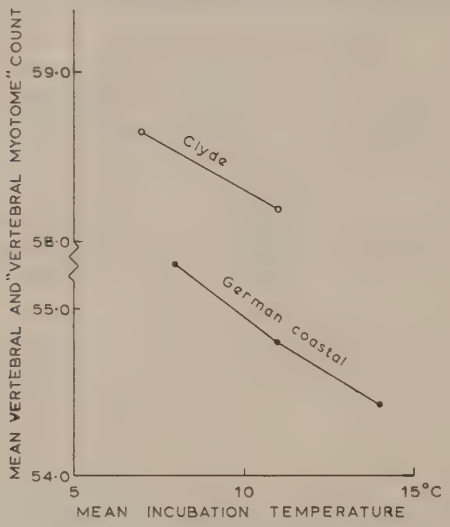

Figure 4. Showing the effect of incubation temperature on mean vertebral and "vertebral myotome" counts.

2. Vertebral and "vertebral myotome" counts

The counts are shown in Table 5 and Figure 4. Both the experiments on German coastal herring and Clyde herring show a significant negative correlation between the counts and temperature. Unfortunately no data are available for either larvae hatched in different salinities or for a Kiel × Clyde cross. The counts of the Clyde offspring were much higher than those of the German coastal larvae. This may be partly due to a genetical effect. However, while the German coastal herring have counts similar to those of the parent race, the Clyde counts are much higher than expected. This could be caused by slightly less favourable conditions prevailing in the Clyde experiments where fresh sea water was not continuously available. GABRIEL (1944) showed that killifish reared in the laboratory had higher vertebral counts than those of wild fish.

Discussion

These results go further than the earlier work of HEMPEL (1953) and BLAXTER (1957) on the experimental modification of meristic characters in herring. Not only do they confirm this earlier work in that incubation temperature has a modifying influence on myotome counts; they also show that salinity before hatching also has such an influence. Further, they suggest that there is a particular sensitive phase before hatching when the myotome count is determined. Perhaps more important, these results give reason to suppose that the vertebral number itself is modified by incubation temperature. Hitherto, this could only be inferred. There is also a suggestion that the difference in mean vertebral counts of Scottish and German spring spawners is genetically based.

So far no evidence has been obtained of a "Tåning effect" in herring, that is the meristic counts being lowest at intermediate temperatures.

Further crossings would be desirable to test the basis of metamerism. For instance crosses should be made between: —

1. Herring of the same area with the same vertebral counts.
2. Herring of the same area with different vertebral counts.
3. Herring of different areas with the same vertebral counts.
4. Herring of different areas with different vertebral counts.

Other experiments are needed to test the sensitive period during incubation when the meristic characters are determined and whether it is the same in all herring groups.

While the influence of the environmental conditions on the meristic characters in herring seems certain, the value of these characters in racial work need not be jeopardized, for as long as the environmental conditions at spawning remain within certain limits the meristic characters will still act as a "label" giving the origin of the herring. One cannot help being struck by the difference in the meristic characters of Scottish and German coastal spring spawners. This difference may be ascribed mainly to genetical causes, for the main difference in environmental conditions for the spawning of these populations, apart from topography, is one of salinity and there is no evidence of this causing a drop in the mean of the vertebral count of about 1·6 vertebrae. This view is confirmed by the results of vertebral and "vertebral myotome" counts described in this paper. There can be no doubt that these German coastal spawners, both in their meristic characters and to some extent in their ecology, have much in common with *Clupea pallasii*.

Acknowledgements

Our thanks are due to Professor A. Bückmann, Dr. C. E. Lucas, and Mr. B. B. Parrish for arranging this collaboration and for the valuable discussions we have had with them. We are also grateful to Mr. W. Hall of the Marine Laboratory, Aberdeen for his help with the statistical treatment of the results.

Summary

1. Rearing experiments were done on herring at Helgoland in 1960, using eggs and sperm from spring spawning herring of the Elbe estuary and Kiel Bight. A successful cross fertilization was also made between the eggs from a Kiel female and the sperm of a Scottish (Clyde) spring spawning male, the sperm having been stored frozen for six weeks. Results are also given of some work done at Aberdeen in 1957, using a Clyde male and female.

2. The eggs were incubated and the larvae reared in the early stage at different temperatures (about 5, 8, 11, and 14°C) and different salinities (5–50 ‰). Samples of larvae were taken at hatching and at the end of the yolk-sac stage for counts to be made of their myotomes. Larvae which survived beyond the yolk-sac stage (a few of which metamorphosed) were fixed on death and counts made of other meristic characters which developed after yolk-sac absorption. In particular counts were made of vertebrae and "vertebral myotomes". The latter are the myotomes which are connected with the formation of vertebrae and which are detectable once the urostylar elements are formed.

3. A significant negative correlation was found between mean myotome count at hatching and incubation temperature, and a significant positive correlation between mean myotome count at hatching and incubation salinity. The mean myotome counts of the Kiel ♀ × Clyde ♂ cross were significantly higher than the Kiel ♀ × Kiel ♂ controls. A sensitive phase was found 6–7 days after

fertilization at an incubation temperature of 10°C when a temperature shock (placing the eggs for 24 hours in 4°C) resulted in a much increased mean myotome count.

4. Significant negative correlations were found between mean vertebral and "vertebral myotome" counts and temperature of incubation in larvae which survived well beyond the end of the yolk-sac stage, both where the parents were German coastal spawners (work done at Helgoland) and where they were Clyde spawners (work done earlier at Aberdeen). There appeared to be a considerable difference between these counts for Clyde and German coastal spawners, which strongly suggested a genetical difference between the groups.

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The Early Life History of the Bonga, *Ethmalosa dorsalis* (Cuvier and Valenciennes)

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Introduction

Ethmalosa dorsalis, a member of the Clupeidae, is one of the most important food fish caught in the coastal waters of Senegal, Gambia, Guinea, Sierra Leone, and Nigeria (BROWN, 1948; CADENAT, 1948). LONGHURST (1960a) has estimated that in 1959 approximately 3,500 canoes were fishing exclusively for this species in Sierra Leone; accounting for 14,000 metric tons, or about 2/3 of the total fish landings of the country. The fishery for *Ethmalosa* in the large estuary known as the Sierra Leone River was investigated by SALZEN (1958) who discussed the breeding behaviour and spawning of the fish from the indirect evidence of length, weight, and maturity estimates. He noted that systematic collections of the eggs and larvae would be needed before any firm conclusions could be reached on these aspects of the life history of the species. However, it must first be possible to distinguish the eggs and larvae of *Ethmalosa* from those of other clupeid fish. This paper presents a description of the development of the egg and the early larval stages of *Ethmalosa*.

Material and Methods

On two nights during November 1956, several ripe male and female *Ethmalosa* were caught in the Sierra Leone River (Fig. 1). The fish were taken by drift nets in the lower reaches of the estuary opposite Freetown at about high water. On each occasion, several hundred eggs were fertilized artificially in large jars. After returning to the laboratory, the eggs were transferred into several aquaria, each of about four litres capacity and containing filtered sea water from the locality where the fish were caught (temperature 27–28°C, salinity 25–30‰). The aquaria were placed in sinks and arranged so that tap water from the mains circulated around them. By this means it was possible to keep the sea-water culture medium at a satisfactory, uniform temperature of be-

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Figure 1. The Sierra Leone River.

tween 26·8° and 27·7°C. The majority of the eggs hatched on both occasions and in an effort to keep the larvae alive, the sea water was changed frequently in some of the aquaria and rarely in others. Greatest success was obtained in the aquaria containing fewer than fifty larvae with the water slowly renewed every twelve hours, using freshly collected sea water from the vicinity where the mature fish were caught. Samples of the developing eggs and larvae were removed at frequent intervals and preserved. The lengths of the larvae were measured from the anterior point on the head to the end of the notochord. All dimensions given in the following account refer to material preserved in 5% formaldehyde.

Development of the Egg

All living eggs floated to the surface of the water in the aquaria and remained there until hatching took place. The egg of *Ethmalosa* is spherical with a smooth and rather delicate capsule. The yolk is segmented though in some eggs individual yolk globules are difficult to distinguish. Most eggs contained a single, small oil globule but in some as many as three oil globules were present close together opposite the animal pole.

Two hours after fertilization, the blastodisc was well advanced being berry-like in appearance with over one-hundred cells (Fig. 2a). At this stage, the eggs had an average diameter of 0·95 mm (range 0·92 to 0·98 mm) and had a perivitelline space between 0·01 and 0·05 mm wide. By ten hours after fertilization, the embryo was well differentiated with a number of myotomes visible in the body and two large eyes in the head. Figure 2b shows the egg fifteen hours after fertilization by which time the embryo almost encircled the yolk

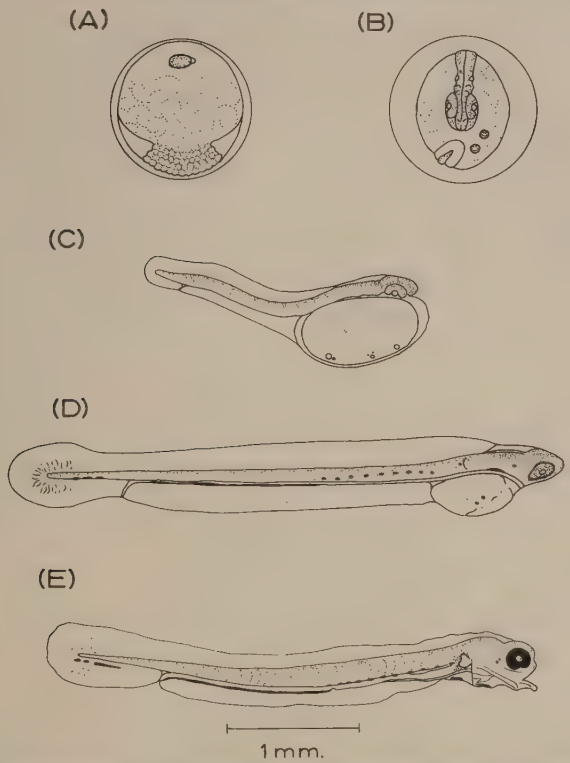

Figure 2. Development of the egg and larva of *Ethmalosa dorsalis*: (A) egg 2 hours after fertilization; (B) egg 15 hours after fertilization; (C) newly hatched larva; (D) yolk-sac larva 24 hours after hatching; (E) larva 60 hours after hatching.

and had a well developed fin fold. The eggs at this stage had increased in diameter to between 1·00 and 1·08 mm with a mean of 1·06 mm, apparently as the result of the absorption of water. This increase in the diameter of the egg capsule, combined with the utilization of yolk material by the embryo, had resulted in an increase in the width of the perivitelline space to between 0·10 and 0·21 mm. Hatching began fifteen hours forty-five minutes after fertilization and by eighteen hours fifteen minutes all the larvae had emerged.

Early Development of the Larva

The average length of the newly hatched larvae was 1·97 mm. As shown in Figure 2c, they were in a relatively undeveloped state, lacking a mouth and without eye pigment. Development proceeded very rapidly and by twenty-four hours after hatching, the larvae had attained an average length of 4·09 mm with

partial absorption of the yolk-sac (Fig. 2d). At this stage, the fin fold and alimentary canal showed considerable development and the eyes were slightly pigmented. Body pigmentation was first observed at this stage in the form of from six to eleven melanophores in a lateral position at the anterior end of the body, a line of pigment under the posterior two-thirds of the gut and patches of pigment ventrally in the caudal region. Thirty hours after hatching, the yolk-sac was vestigial or had become completely absorbed. The larvae had an average length of 3·94 mm which represents a slight decrease below the length at the previously described stage. The eyes were pigmented and two of the three pairs of otoliths were visible. The mouth was open with the lower jaw developed and, in the gut, the pylorus had differentiated.

The mortality rate of the larvae increased rapidly sixty hours after hatching and it was apparent that none would survive much longer so approximately fifty of the more active ones were preserved. All the larvae had died at eighty-five hours after hatching. Figure 2e shows the appearance of a larva sixty hours after hatching. It was more heavily pigmented than the yolk-sac larva with patches of pigment under the heart and close to the cleithrum. A ventral migration of the lateral melanophores had also taken place, resulting in a row of between six and eleven melanophores on each side just above the fore gut. A line of pigment ran along the ventral side of the gut posterior to the pylorus and dashes of pigment were present around the anus and in the caudal region. The average values of the various counts and measurements made on the most advanced larvae from the aquaria are listed below: —

Standard length from the anterior point on the head to the end of the notochord	3·47 mm
Length from the anterior point of the head to the anus	2·83 mm
Length from the anterior point of the head to the pectorial symphysis	0·50 mm
Number of myotomes from the cleithrum to the anus	35·7
Total number of myotomes visible in the body	40·3
(Myotomes in the tail region were indistinct)	
Average number of melanophores on each side of the fore gut	8

The Clupeid Larvae of the Sierra Leone River

It is generally recognized that one of the most useful characters for separating different species of clupeid larvae is the total number of myotomes in the body, the number of myotomes being related to the number of vertebrae.

Ethmalosa dorsalis has an average of about 43 vertebrae (POSTEL, 1950) and therefore its larvae should be distinguished easily from those of *Sardinella* spp. which have an average of 46 or more. Both *S. cameronensis* Regan and *S. eba* (C. and V.) have an average of about 46 vertebrae (REGAN, 1917b; ROSSIGNOL, 1955) while *S. aurita* (C. and V.) has about 48 (MAINGUY and DOUTRE, 1958). There are, however, two common species of clupeid fish found in the coastal waters of Sierra Leone which have vertebral numbers closely similar to *Ethmalosa*. These are *Pellonula vorax* (Günther) which has about 42 vertebrae (REGAN, 1917a) and *Ilisha africana* (Bloch) which was found to have between 42 and 43 (only four specimens examined).

A comprehensive investigation of the plankton of the Sierra Leone River and the sea off the mouth of its estuary was carried out during 1954 and 1955 (BAINBRIDGE, 1960). During this survey a large variety of fish larvae were collected by means of standard oblique hauls using a 50 cm diameter tow net (10 meshes per cm). The two stations shown in Figure 1 were worked at approximately weekly intervals. Station A situated at the mouth of the estuary was sampled at high water and Station B in the central region of the estuary was sampled at low water. The collection of fish eggs and larvae was continued throughout 1959 and 1960 by Mr. A. R. LONGHURST who has kindly allowed me to examine his samples. These latter collections were made with a high-speed plankton sampler over a wide area which included the extreme upper reaches of the estuary not covered during the previous survey of 1954–55. With all this material available, it was hoped that it would be possible to extend the growth series from the artificially reared larvae to more advanced *Ethmalosa* larvae from the plankton samples. However, none of the clupeid larvae taken during these surveys were of this species.

All the clupeid larvae taken off the mouth of the estuary at Station A form one continuous growth series. The largest specimens were stained in alizarin and found to have an average of 46 vertebrae. From the number of fin rays of the dorsal and anal fins, which are fully developed in the largest specimens, they have been referred to *Sardinella eba*, by far the most abundant species of *Sardinella* in the coastal waters of Sierra Leone.

All the clupeid larvae taken within the estuary at Station B also form one continuous growth series. Counts made on some of the largest specimens after staining with alizarin showed that they had an average of 42·2 vertebrae. These larvae were confined to the estuary and only appeared at Station B during the wet season, a period when *Ethmalosa* is absent or very rare in the region. On the basis of fin-ray counts made on some of the largest specimens it has been possible to refer them to *Pellonula vorax*, a small clupeid fish which is most abundant in the numerous creeks and extensive shallows of the upper reaches. The larvae of *Pellonula* had presumably been swept into the central region of the estuary by the increased run-off from the land during the wet season.

Discussion

The fishery for *Ethmalosa* in the Sierra Leone River employs both cast and drift nets. Landings are greatest during the dry season (November–June) and fall off to negligible quantities during the wet season (July–October). Large numbers of juvenile *Ethmalosa* (known locally as "awefu") are found among the shallow creeks in the upper reaches of the Sierra Leone River. The modal length of juveniles from fish fence traps is about 12 cm but individuals as small as 3–4 cm are found in the catches of women's hand nets. However, the absence in the estuary plankton, of eggs or larvae which can be attributed to *Ethmalosa* is very strong evidence that no appreciable spawning takes place in the region. Recent tagging experiments described by LONGHURST (1960b) suggest that a considerable exchange of individuals or shoals takes place between the estuary and offshore banks as far north as the border with Guinea. It therefore seems likely that spawning takes place in the vicinity of these shallow offshore banks and that after metamorphosis the young fish migrate inshore. This hypothesis

agrees well with the observations of BLANC (1948) and POSTEL (1950) on the fishery for *Ethmalosa* off Senegal. Here shoals of immature *Ethmalosa* are present in the estuary of the Saloum during March and April and large concentrations of spawning fish are found in the region of the offshore bank of Joal during August and September.

BAINBRIDGE (1957) found that adult *Ethmalosa* are relatively non-selective feeders and that those caught within the estuary during the dry season are feeding intensively on phytoplankton. It is also known that the fat content of fish from the estuary increases from less than 10% of the dry weight in January to more than 20% during June and July (WATTS, 1957). The aggregation of *Ethmalosa* in the Sierra Leone River during the dry season is therefore probably a feeding aggregation associated with the very high standing crop of diatoms which develops in the region over these months (BAINBRIDGE, 1960).

Finally, it is to be noted from this present work that the spawning habits of *Ethmalosa* differ from those of the shads. Both the European and American shads (genus *Alosa*) and the Indian shad (genus *Hilsa*) are anadromous fish, ascending rivers to spawn and laying demersal eggs. Several publications in English refer to *Ethmalosa* as the "West African shad" but it would be more appropriate to retain the name "*bonga*" which is widely used in many parts of West Africa.

Acknowledgements

I wish to thank Mr. A. G. TAYLOR, Director of the West African Fisheries Research Institute who carried out the artificial fertilizations and Mr. A. R. LONGHURST for the loan of material and for his helpful advice during the course of the work.

Summary

1. Ripe males and females of the clupeid fish *Ethmalosa dorsalis* (C. and V.) were caught and the eggs were fertilized artificially. The development of the egg and the early life history of the larva are described.

2. The eggs and larvae of *Ethmalosa* were not found in the plankton of the Sierra Leone River. It is suggested that spawning takes place in the vicinity of offshore banks and that the fishery for *Ethmalosa* in the Sierra Leone River depends on a feeding aggregation of the species.

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Reviews

Erich Bruns. "Ozeanologie. Band 1: Einführung in die Ozeanologie. Ozeanographie". 420 pp., 145 figs. Veb. Deutscher Verlag der Wissenschaften. Berlin, 1958. DM 41.

The book under review is the first volume of a work which is planned to run to 4 volumes and in which the author intends to give the latest results in all branches of oceanography, together with the historical development of a number of oceanographical problems and the development of oceanographical instrumentation.

The first 5 chapters of this volume form an introduction to oceanography, defining the place of this branch of geophysics in relation to other branches, and dealing with its development as a science. There is a chronological list giving a number of facts about some 300 oceanographic expeditions (years, ship, country, Leader of expedition, working area, and main objectives).

The rest of the volume deals with what the author calls "Ozeanographie", i.e., the establishment of the topography of the basins of the water masses, although a short account of the oceanographical characteristics of the waters filling up the basins is also included. This main part of the volume falls into three sections.

The first section deals in 2 chapters with the dimensions and types of the different oceans and seas, as well as with their depth conditions.

The second section is of 6 chapters and gives the basis for survey work and the methods and instruments used in this work: the ship and the general basis for navigation; sea charts; nautical books; basic methods of navigation; hydrographic survey; methods and implements for establishment of the bottom topography in the open sea and in coastal areas.

The third section comprises 9 chapters and gives short accounts of the oceanographical characteristics of the 4 oceans and 54 seas as well as the Caspian Sea, the Aral Sea, and Lake Baïkal. For each area the following matters are dealt with: bottom topography and geological nature of bottom; currents; sea level fluctuations (tides); waves; temperature, salinity, and density of the water; ice conditions; transparency, colour, and other physical properties; further chemical properties.

The reviewer finds the book very useful. The section containing the oceanographical characteristics of oceans and seas is most valuable as it gives, in one place, a great variety of information which would otherwise have to be picked up from many different sources, several of them in the Russian language. Although the characteristics given for each sea are short, they will suffice for many purposes.

A number of lists and indexes (covering 62 pages) adds to the value of the book. Thus there is a geographical index, an index of authors cited, and a detailed subject index.

Volume II is planned to cover "Ozeanometrie", i.e., it should deal with the methods of oceanographical measurements and the instruments and tools used for these measurements, together with the processing of the data. Finally, Volumes III and IV are planned to cover "Ozeanologie", i.e., oceanography proper.

Jens Smed

R. Vibert & K. F. Lagler. "Pêches Continentales: Biologie et Aménagement". pp. 720; 164 figs.; 52 pp. de références. Dunod, Paris, 1961. 88 NF.

This book on inland fisheries ranges over a very broad area of knowledge. The first part starts with the principles of ecology, the transfer of energy, the units of population and the effects of environmental factors on aquatic organisms. Chapter 6 carries on with the study of a population, considering age-groups, aggregations, growth, competition, simple mortality and density dependent mortality; chapter 8 is concerned with the mathematical theory of fishing as developed at the Fisheries Laboratory, Lowestoft. The second part of the book treats of management, the detection and control of pollution, the construction of fish passes and shelters, the fertilization of waters, the control of predators and disease, the stocking of lakes and rivers and the exploitation of freshwater fisheries. The third part deals with special techniques like pond culture, brackish water lagoons, and "vallicoltura". In the fourth part, certain techniques are set out, statistical techniques, marking techniques, market records, the sampling of age and growth, and methods for the ecological diagnosis of fisheries. Each section is concise, with a full list of references.

In such an extensive field I am competent to criticize only small parts. The definitions in the section on ecology and ecosystem did not convince me, but one subheading in this chapter did: "la mort, clef de voûte de l'ecosystème". Table 3:1 gives the efficiency of energy transfer in an ecosystem; this material was familiar to me in origin, but assembled in one place it is most forceful. Table 3:2 gives primary production in kg/hectare/year of carbon on land, in fresh water, and in the sea; Table 3:3 gives kg/hectare of fish caught in the sea, in lakes, in fertilized and in unfertilized fish ponds. Such tables set the scale of working for a fisheries ecologist.

Considering the study of populations, growth (G) is defined as dw/dt in weight; so is mortality (Z). Obviously the first is a positive coefficient and the second is a negative one; the slight confusion might have been avoided if growth in weight and mortality in numbers were separated as in the theory of fishing. The authors treat population theory separately from the theory of fishing; it is made very clear that the mathematical theory of fishing is a more powerful method of population analysis than that method based on the logistic curve found in many ecology textbooks.

The section on fish culture covers Chinese carp culture, German carp culture, ricefield culture, the culture of *Tilapia* in Indonesian tambaks, etc. The use of fertilizers is fully discussed. I was unable to find how to start a trout farm as developed in Denmark.

In the technical section at the end, variances and standard errors of means are calculated; confidence limits to the difference of means are calculated and methods of sampling, including stratified sampling are discussed. The method of least squares, correlation and the χ^2 test are described. Figure 17.1. shows all types of fish marks that I have heard of. Figure 18.1. shows the limits of the Petersen method of age determination by length frequencies, i.e. that it works well in the younger age-groups, but not so well in the older age-groups where the distributions of length overlap. LEE's phenomenon is attributed to differences in growth-rate: JONES (1958) has explained it in terms of fishing mortality.

The bibliography on the theory of fishing includes the chief works of RUSSELL, GRAHAM, THOMPSON, RICKER, BEVERTON and HOLT, SCHAEFER, WIDRIG and GULLAND; BARANOV (1918) is not included. Pictures are clear and good, particularly those of the amateur fishermen, sporting and sedentary; tables and figures are clearly set out. By now it must be obvious to the reader that I liked this book.

D. H. Cushing

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